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Alternative Approaches to the Identification and Reconstruction of Paleoecology of Quaternary Mammals

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Alternative Approaches to the Identification and Reconstruction of Paleoecology of Quaternary Mammals

by

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Dedication

To Ernie for his inspiration and an often much needed cup of coffee,

To my family for all of their love and encouragement,

And especially

To Heather

Thank you all for believing in me.

Epigraph

To the question which here so naturally presents itself, as to what might have been the climate of the northern hemisphere when peopled with genera of animals which are now confined to the warmer regions of the earth, it is not essential to the point before me to find a solution; my object is to establish the fact, that the animals lived and died in the regions where their remains are now found, and were not drifted thither by the diluvian waters from other latitudes.

-William Buckland, 1824, *Reliquiæ diluvianæ*, p. 44.

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Alternative Approaches to the Identification and Reconstruction of Paleoecology of Quaternary Mammals

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Since the 19th century the remains of Quaternary mammals were an important source of data for reconstructing past environmental conditions. I tested two basic assumptions that underlie Quaternary vertebrate paleoecology. The first assumption is that fossils mammals can be identified reliably to species. The second assumption is that correlations established between extant mammals and environmental parameters can be used to interpret reliably the paleoenvironment from the latest Pleistocene.

Incorrect specimen identifications could lead to errors in paleoecologic interpretations. I explicitly tested an alternative to the traditional approach to identification by identifying fossil shrews based on apomorphies. My results indicated that some traditional characters are useful for identification, but only complete specimens with a combination of characters can be identified to species. This indicates that previous

authors who identified shrews to species did not compare them to the full diversity of species.

I tested the reliability of cenograms and species-richness models as approaches for the reconstruction of environmental conditions in the past. I used faunal data from Hall's Cave, Kerr County, Texas to construct cenograms and species-richness models and compared the results to independent paleoclimate proxies. Neither species-richness models nor cenograms agree with paleoenvironmental reconstructions based on proxy data from the Late Pleistocene and Holocene. Cenograms and species-richness models are unreliable and fraught with problems, and both approaches should be abandoned as tools for paleoecological reconstruction.

To test for potential geographic bias in the identification of Quaternary fossils I developed a GIS (geographic information systems) database of Quaternary paleontological sites within Texas. I was able to show that the identification of species of fossil soricids, heteromyids, *Odocoileus*, and *Spilogale* was influenced by geography. Those fossils should be treated as generic identifications until they are re-evaluated against the full diversity of species. Utilizing GIS I also developed a method of paleoecological analysis. My analysis showed that the environmental conditions found today in Texas might not be limiting the current range of shrews. Based on the known geographic range of shrew fossils, other ecological factors besides environmental conditions are shaping the current distribution of shrews.

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CHAPTER 1: INTRODUCTION: HISTORIC RESEARCH AND CONTEMPORARY QUESTIONS IN PALEOECOLOGY

My research questions were motivated by my perception that some of the basic assumptions made by Quaternary vertebrate paleontologists could have profound effects on the ability to recover meaningful paleoecological interpretations from the fossil record. My first objective was to test the degree to which apomorphic identification of fossils yield different taxonomic resolution compared to identification based on morphologic similarity that may be refined by geographic and temporal criteria. Secondly, I wished to document the consequences for Quaternary paleoecological reconstructions if species-level identifications are unreliable or unattainable and higher-level taxa are used to make interpretations. These significant questions need to be evaluated because every subsequent hypothesis is dependent on the identification.

I next looked at paleoecologic interpretations of Quaternary mammals, particularly how they related to paleocommunities of mammals. A paleocommunity is a group of organisms living in close geographic and temporal proximity. I explored several questions. What kind of change, if any, occurred in the mammal paleocommunities in central Texas from the Late Pleistocene through the Holocene? Can change in the paleocommunities, such as relative or absolute abundance of taxa be correctly interpreted as a change in the paleoecology of organisms or communities? If there are changes between Pleistocene and Holocene paleocommunities, can these be interpreted as changes in the environmental requirements (habitat and climatic tolerances) of organisms or their relationships to other organisms (community structure and biologic interactions)? Is using the modern ecological parameters (as best as they are known) of

an organism to interpret its paleoecology a good approximation, or is there significant evidence that the ecological parameters of organisms have changed significantly through the Pleistocene and Holocene?

Though at the time they were not formally defined, both ecology and paleoecology have their roots in the 19th century. Paleoecology is the study of ecological interactions of organisms and their environment in the past. Even before paleoecology was a recognized field people were fascinated by the two basic, related questions that form the foundation of paleoecology: how did the ancient organisms interact with other organisms and the environment, and what was the environment like in the past? Early naturalists such as Buffon and Haeckel began to formalize the study of the relationship between organisms and their environment, which forms the foundation of ecology (Fenton, 1935).

However, it is not clear, whether paleoecology can be seen as a direct application of ecology to the fossil record. Several problems make it difficult to directly apply ecology to fossils. First, the time scales of ecological phenomena, as currently understood, are vastly different from the time intervals that are generally resolvable in the fossil record. Second, taphonomic biases can alter the taxonomic composition of any fossil deposit so that the fossils may not accurately represent the community that inhabited the area prior to or during deposition. Another potential issue is that the ability to identify fossils to species is generally not the same as extant taxa. If this is the case, what are the limits on the type and degree of ecological analyses that are possible? All of the potential complications are important, but are often overlooked in paleoecological analysis. I endeavored to address these issues in this dissertation.

RECONSTRUCTING PALEOENVIRONMENTS

I chose to investigate the paleoecology of Quaternary sites because they commonly have a greater wealth of taxa and better preservation than sites from older geologic periods. One of the earliest examples of the scientific study of Quaternary cave deposits was published by William Buckland first in the *Philosophical Transactions of the Royal Society of London* (Buckland, 1822), and then reproduced in a larger work, *Reliquium Diluvianae* (Buckland, 1824). Though Buckland's theoretical perspective was firmly entrenched in a catastrophist view, he demonstrated that the presence of bones in the caves was caused by natural phenomena, namely the denning behavior of hyenas. His paleoecological contribution was to note that there were four groups of mammals present together in the cave, rhinos, elephants, hippos, and hyenas that occur far to the south in much warmer climates at present (and only occur together in southern Africa). He considered that their presence could indicate that climate was much warmer in the past or that the animals tolerated cooler climates in the past. Based on other tropical taxa, such as crocodiles he decided the climate was likely warmer at the time the fossils were deposited in the cave.

Early in the history of paleoecology most of the research was directed towards reconstructing past environments. As was noted by Fenton (1935), ecology is the study of the relationship of organisms to their environment. It encompasses single organisms, groups or communities of organisms, and the biotic and abiotic aspects of the environment. Paleoecology also embraces these areas of study, but is complicated by the nature of the fossil record.

Two areas of ecology are most important for paleoecology. The first is the relationship of organisms to their environment, and the second are the relationships between organisms. These are expressed as paleoenvironmental reconstructions and

community paleoecology. There is wide agreement on these aspects of paleoecology (e.g., Fenton, 1935; Shotwell, 1955; Cloud, 1959; Olson, 1985; Jablonski and Sepkoski, 1996)

By mid-late nineteenth century, it was widely accepted that there were significant differences between the previous faunas and those of the Pleistocene. Repeated events of continental glaciation were first recognized by Louis Agassiz (1840). The widespread acceptance of continental glaciation influenced subsequent authors to emphasize the roll that climate played on influencing the current distribution of mammals (Cope, 1871). As was understood at the time, the present distribution of the biota was largely driven by past climatic conditions, but less so by the current conditions (Adams, 1905). This was an early example of the recognition of the importance of the historical dimension of paleoecology. Adams drew examples from fossils of arctic mammals that were found where temperate zones exist today. He discussed reconstructing the past succession of changes to the environment to describe how the one preceding it influenced each subsequent fauna.

W. D. Matthew's *Climate and evolution* (1915) was one of the most influential early works that secured the idea that cyclic climate change was the significant contributing factor to the evolution and distribution of terrestrial vertebrates. He thought that all dispersal happened from the Holarctic, and that only minor geographic changes could explain the present distribution of vertebrates. This was due to the idea that the continents were fixed geographically. He thought that land bridges between continents were caused by both changes in eustatic sea level due to climate change, and isostatic changes in the elevation of continents. His perspective was that as environments shifted, the animals (and plants) moved with them, or remained in place and adapted to new conditions. Those ideas strongly influenced succeeding paleoecologists.

By the middle of the twentieth century, it was accepted that most of the extant terrestrial species of plants and animals originated in the Pliocene or before. It was then the climatic changes in the Pleistocene that led to the present day distribution of the biota (Deevey, 1949). Much of the research focus on the relationship between mammals and climate shifted from determining the cause of the present distribution of mammals to using various groups of mammals to make paleoenvironmental interpretations of Quaternary deposits (e.g. Hibbard, 1953; Guilday et al., 1964; Grayson, 1987; Winkler, 1990, Hadly, 1999). In those papers, mammals were used to describe in general terms how the paleoenvironment was warmer or cooler, or wetter or drier from the present because of the presence or absence of certain mammal taxa.

However, in the early 1920's it was cautioned that the primary data used to reconstruct past environments should be from inorganic substances (Case, 1921). Case suggested that both inorganic and organic materials should be used in conjunction. In addition, he argued that plants provide better paleoenvironmental information because they are immotile during their life. He was referring to macrobotanical remains. Pollen is the most commonly used plant remains for paleoecology, but is highly mobile.

An important theoretical contribution to conceptualizing the reconstruction of paleoenvironments was Hutchinson's theory of multi-dimensional niche space (Hutchinson, 1957). That was a theoretical model developed to describe how each organism within a community was limited by various environmental parameters such as temperature, moisture or salinity. In the model each environmental variable contributes to limiting the range of habitats available to a species. This type of niche theory describes the environmental requirements of a species. This is opposed to the other type of niches that describe the role a species plays in an ecosystem (Leibold, 1995).

Ideally, if all of the limiting factors were known for each organism in the community then the environmental conditions of the ecosystem would be constrained precisely. Unfortunately, this is never the case; all of the limiting factors of extant organisms are not known (Martin, 2001). Hutchinsonian niche theory is no longer widely accepted among ecologists as the dominant organizing force of communities (Leibold, 1995). While limiting factors are still recognized as important ecological criteria, most of the focus in niche theory has shifted to the "role" that a species plays in a community.

This would suggest that physical environmental conditions are not solely responsible for faunal change. Much early work by paleontologists in the field of paleoecology focused on large-scale patterns of continental biomes and the influence that glaciation had on the biota (e.g., Cope, 1871; Adams, 1905; Matthew, 1915; Fenton, 1935). However, contemporary botanists and paleobotanists were more interested in the biotic interactions between plants and the organization of plant communities (e.g., Clements, 1916; Gleason, 1926; Phillips, 1931; Clements, 1936).

COMMUNITY ECOLOGY

My operational definition of a community is a group of organisms living in close proximity (Fauth et al., 1996). Communities were defined at a great range of scales and have represented arbitrary or natural groupings (Strong et al., 1984). There is added complexity when dealing with the fossil record because an ecological community should represent a contemporaneous group of organisms. Communities are the (purported) functional level of most paleoecological studies. It was noted by Olson (1966) that most paleocommunities in his works were only related in a broad sense to the communities

from which they were derived. This is likely the case for most paleocommunities, especially terrestrial vertebrate paleocommunities, except for rare cases of extraordinary preservation. When trying to define a paleocommunity both geographical proximity and the temporal proximity must be considered. Therefore, an understanding of the deposition mode and the time averaging of the deposit are essential for determining the relationship between the ecological community and the paleocommunity that was preserved (Fagerstrom, 1964).

Community Organization

Two theoretical models that attempted to explain the organizing patterns of communities were developed from studying ecological succession. Clements in a series of papers starting with, *Plant Succession* argued that plant associations (or communities) function like organisms (Clements, 1916). His view was that all plant succession led to the same association of species because there was a higher-order organizing factor that shaped plant communities (Clements, 1936).

There was immediate criticism of some of Clements's interpretation of paleoecology. Clements accepted that the modern flora can be used to interpret pre-Cenozoic communities without question, but there are a number of problems with this view. First, pre-angiosperm plants would have significant differences in dispersal. Second, there were likely differences in the concentration of atmospheric CO_2 at various times in the past and this would have a noticeable effect on plants (Seward, 1917).

By the 1930's, ecologists routinely discussed plant and animal communities separately. It was advocated by Phillips (1931) that a biologic community should be more frequently discussed. His argument was against treating plants and animals as separate

communities because there is interaction between them and they could be treated as members of the same community. This idea was advocated by Clements. He concluded that ecological studies of communities include as broad an aspect as possible (Clements, 1916).

Though Clements's views about ecological succession and community organization were well accepted, an alternative model of plant succession was advocated by Gleason (1926). Gleason argued that every variation in the environment through time led to greater and greater differences between associations. There was no overall organizing factor each individual species, and each was affected by successional parameters differently. It took a number of decades until Gleason's individualistic community theories were widely accepted (Gleason, 1987).

Both Clements's and Gleason's models of community organization can be thought of as end points on a continuum between fully interacting 'organism-like' communities and communities as independent associations of organisms. There is a large amount of evidence that communities of both plants and animals have different associations of species between the Pleistocene and the present. This suggests that community organization was predominantly shaped by individualistic species responses when comparing Quaternary communities to the present (e.g., Lundelius, 1989; FAUNMAP Working Group, 1996; Jablonski and Sepkoski, 1996; Stafford et al., 1999; Jackson and Williams, 2004; Lorenzen et al., 2011)

Non-analog Quaternary Communities

A non-analog community or fauna is one that includes an association of extant species that are found together in Pleistocene (primarily) deposits, but are separated by

hundreds of miles or more today. This means that there is no modern analog to the association of species at most Pleistocene sites. There are many examples of non-analog faunas from all over the world (Lundelius, 1989). One proposed cause of non-analog faunas is that species responded in a Gleasonian (individualistic) manner to the environmental changes that happened over the last glacial-interglacial transition. It was noted by Lundelius (1989) that mammals can change their tolerances of environmental conditions but are, at least for herbivorous mammals, closely tied to plants that they eat. Plants in turn have a stronger relationship with climate than do terrestrial animals. Typically, non-analog faunas are interpreted to be the result of greater environmental heterogeneity. The results of several analyses of Quaternary sites across North America found that although individual species might have responded to climate change in idiosyncratic ways, the larger scale biotic provinces remained intact from the Late Pleistocene to the Holocene (FAUNMAP Working Group, 1996; Lyons, 2003). Non-analog faunas had a large taxonomic diversity in disharmonious associations. This would suggest that in the present those species are likely not occupying the full range of environmental conditions they are capable of occupying (Lundelius, 1989).

An important but previously over-looked cause of non-analog faunas could be extinct populations (Stewart, 2009). This is a significantly different interpretation than the standard interpretation of more equitable climate (FAUNMAP Working Group, 1996). If the extinct populations had different environmental tolerances, it would explain different associations of species than are seen today. As discussed by Stewart (2009), the extinction of those populations would have a potentially significant evolutionary effect. The loss of the genetic diversity of those populations would render the species more susceptible to extinction because of climate change.

IMPORTANCE OF PRECISE IDENTIFICATION

The precision of any paleoecologic interpretations is at the mercy of the quality of the identifications of the fossils. The quality of Quaternary fossil mammal identifications is a major concern. Commonly, Quaternary fossils are identified by comparing the morphologic similarity of a fossil with other fossils or extant specimens from the same region in which the fossils were found. Though common, this can lead to a series of potential problems with later interpretations. Fossils that are identified with the aid of geography will bias the interpretations that are drawn from them by obscuring the changes in distribution through time (Cloud, 1959; Bell et al., 2010). Using geography or time to aid in the identification of fossils is usually a hidden assumption that is not explicitly stated in discussions of how fossils were identified.

An insightful discussion of the problem of geographical bias in the identification of Quaternary fossils was undertaken by Stewart (2005). He pointed out that the identification of Quaternary bird fossils in Europe significantly relies on geography to narrow the comparison species. He also discussed that there is little effort in published accounts to describe the role that geography played in identification. There is often some reliance on geography to narrow the number of comparison species, but this should be discussed as a component of the identification and not ignored.

One possible way to address the issue of geography in the identification of Quaternary fossils is to base the identification on apomorphic characters. The use of apomorphies in the identification of small mammal fossils remains largely unexplored, but for a few important examples (Bell and Bever, 2006; Jass, 2009; Bell et al., 2010). Often the characters used to identify taxa are similar (if not identical) between the traditional method of identification and apomorphic identification. However, the ability to discriminate species based on traditional characters may dissolve when fossils are

compared to a sample of species that encompass a larger geographic or temporal sample. The use of geography to restrict the pool of species or specimens used for comparison is the greatest differentiation between an apomorphic approach and the traditional means of identifying Quaternary fossils. Another advantage of apomorphic characters is that they provide a common set of criteria for identifying specimens for paleontologists and mammalogists. This maximizes the ability of both groups to share data.

There is the potential that apomorphic identifications may increase the number of recognized species. This technique yielded greater taxonomic resolution in Mesozoic faunas (Nesbitt and Stocker, 2008). However, there are differences between Mesozoic and Quaternary fossil specimens in both the fossil material that is collected and the methods used to identify them. In many cases, fragmentary, isolated Triassic fossils were originally left unidentified or only identified to higher taxonomic clades such as Archosauria (Nesbitt and Stocker, 2008). Many Quaternary small mammals fossils are assumed members of extant genera or species, and there is an expectation that even isolated teeth and jaws can be identified to species by comparing them to specimens of extant taxa. Though Quaternary small mammals often are recovered by screen washing, and identified as elements, by identifying the fossils with robust apomorphies drawn from a geographically diverse set of specimens it is possible that new or different species will be recognized in faunas that were originally identified with narrow geographic assumptions.

A third advantage to apomorphic identification is that it can place the identified specimen directly into a phylogeny when incorporated into a phylogenetic analysis. Placing specimens in a phylogenetic framework, allows for asking evolutionary questions. The ability to diagnose a fossil to any taxonomic level, even if it is not to species, makes the specimen more valuable because it can still be used to make additional interpretations (Rowe, 1987). In some cases, apomorphic characters will diagnose a particular specimen

to a phylogenetic node in between genus and species. In this way apomorphic characters would provide better taxonomic resolution than other identification methods.

PALEOECOLOGY AND ECOLOGY ABOVE THE SPECIES-LEVEL

It was recognized by ecologists that there needed to be a balance between taxonomic resolution and ecological interpretations. For many taxa, there is a lack of taxonomists capable of identifying large samples of organisms to species. However, community ecology can be still interpreted with higher-level taxa (e.g., Warwick, 1988; Somerfield and Clarke, 1995; Nielsen et al., 1998). These ecological studies of extant organisms are highly relevant to paleoecology because fossils can also be challenging to identify to species. The inability to identify specimens to species does not preclude them from being utilized in paleoecological analyses.

In particular, there are many challenges to identifying Quaternary small mammal specimens to species. Although there is some evidence that higher-level taxa are not useful for detecting environmental change (Grimbacher, 2008), other studies have shown that the generic level is still useful for biodiversity studies of extant mammals (Grelle, 2002). If Quaternary mammal fossils cannot be reliably identified to species, it would be more appropriate to treat species identifications as generic identifications when they were published without reproducible descriptions of how the species were identified. It was argued that the recovery and sequencing of ancient DNA should become common and affordable, thus aiding the identification of species from fossils (Rull, 2012). Until that happens, paleontologists will have to rely on the morphology of the fossils for identification. This was one of the major impetuses of my dissertation. I wanted to

improve the accuracy of identifications of Quaternary small mammals and to recognize when published species identifications were possibly inaccurate.

SUMMARY OF THE DISSERTATION

There is a long and distinguished history of paleontological research in Texas. Beginning in 1920, the first paleontological investigation of the Pleistocene and Holocene of central Texas was undertaken by O. P. Hay. Since then, other paleontologists identified and studied 37 localities on or near the Edwards Plateau (Lundelius, 2003). My dissertation builds on that prior work with the focus of expanding our understanding of mammalian paleoecology, and testing some basic assumptions of the methods of Quaternary paleoecology.

Chapter 2 – Apomorphic identification of shrews

I began my dissertation by explicitly examining the methods of identifying one group of Quaternary mammals. The group I chose was North American shrews (Soricidae). Shrews are a common component of Quaternary faunas, and are often used in paleoecological analyses. I first developed a suite of apomorphic characters to identify shrews from upper and lower jaws. 1 then tested whether identifications based on apomorphic characters have the same level of resolution that previous authors reached when they used gross similarity, whether in conjunction with geographic assumptions or without. It is essential to have a well-defined methodological framework to make research reproducible. A clear understanding of the methods used to identify specimens will allow other scientists to have a better understanding of the interpretations derived from the data. Reproducible methods will allow the identifications to be used in a manner

consistent with the author's intention, and it needs to be explicitly stated to what degree the identification is based on geography and time.

I described 40, potentially apomorphic characters that can be used to identify shrews. By mapping these characters onto phylogenetic trees I determined which were useful as synapomorphies and autapomorphies. By using apomorphies to identify the shrews from Hall's Cave, Kerr County, Texas, I was able to recognize more species of *Blarina* than were recognized using traditional identification methods. However, fewer specimens of shrews were identifiable to species. For *Sorex, Notiosorex,* and *Cryptotis* known apomorphies cannot discriminate species, so any method that relies solely on morphology and does not use geographic distributions of extant taxa to restrict the species used for comparison will not recover species of these genera.

Chapter 3 – Problems with cenograms and species-diversity models

In chapter 3, I investigate two methods of paleoenvironmental reconstruction that attempt to go beyond a qualitative description of paleoenvironment using mammalian faunas. The two approaches were developed that use only the species of mammals from a fossil locality to reconstruct the paleoenvironment from the nearby area. The first approach was cenograms, which were purported to show the aridity and the canopy cover of a paleoenvironment. The second was species-richness models, which claim to yield precise paleoclimatic values for temperature and precipitation. I carefully examined the claims that both approaches accurately reconstruct past environments.

I tested the approaches using a well-studied faunal sequence that spans the Late Pleistocene and Holocene, Hall's Cave. My tests revealed a number of problems with the basic methodology of these approaches. In addition, the paleoenvironmental predictions

of species-richness models and cenograms disagree with the predictions of independent proxies that are not based upon mammals. Cenograms and species-richness models are based on fundamentally flawed assumptions about the relationship between mammals and climate. I recommend that both approaches be abandoned as a technique for reconstructing paleoenvironment, and that the assumption that mammals can be used directly as a paleoenvironmental proxy be re-examined.

Chapter 4 – GIS analysis of Quaternary sites

Ultimately, I want to utilize GIS to test predictions of the effect of paleoclimate on Quaternary mammals, and this chapter represents the first steps towards using GIS to make paleoecologic interpretations. I demonstrated that GIS was a powerful tool for analyzing the degree to which factors such as geology, age, precipitation, or hydrography influence Quaternary site location (Jass and George, 2010). To expand upon that work, I wanted to better quantify those properties that regulate Quaternary site distribution in Texas in order to determine if GIS could be used to investigate aspects of Quaternary paleoecology. Because GIS analysis uses spatial relationships, I first ascertained which factors influenced the location of Quaternary sites using the FAUNMAP database. My work investigating the identification of fossil shrews led me to question some of the identifications in the FAUNMAP database. I developed a new approach using GIS to help determine where fossils were potentially identified to species based on geographic assumptions. I also tested the potential for using taxonomic levels above the species to make paleoecological interpretations when species identifications are not accurate.

Using GIS I found several taxa that were potentially identified to species by using geography to restrict the number of species which were compared to make the

identification. The Quaternary distribution of the genera of shrews in Texas showed that they had different environmental tolerances than today. I concluded that paleoecological analysis does not need to be done at the species level.

CHAPTER 2: APOMORPHIC IDENTIFICATION OF NORTH AMERICAN SHREWS (SORICIDAE: SORICINAE)

INTRODUCTION

Classification and taxonomy

Soricidae includes all extant shrews, has a global distribution, and its members occupy a wide variety of environments from the arctic to the tropics. In North America, five genera of shrews have been recognized since 1950 when Hibbard (1950) separated *Megasorex gigas* from *Notiosorex*. These are *Blarina*, *Cryptotis*, *Megasorex*, *Notiosorex,* and *Sorex* (Figure 2.1). The extant Soricidae were long divided into two subfamilies, Crocidurinae and Soricinae, based primarily on the characteristic that soricines have red-pigmented teeth and crocidurines lack pigment (Repenning, 1967; Wolsan and Hutterer, 1998). More recently, it was suggested that a third subfamily, Myosoricinae, be taken out of Crocidurinae (Hutterer, 2005).

Soricinae, the only subfamily found in North America, was divided into three tribes by Repenning (1967); these were the Soricini, Blarinini, and Neomyini. Repenning's classification was based primarily on the morphology of the mandibular condyles. Recently the tribes were defined as monophyletic groups recovered from molecular phylogenies (Ohdachi et al., 2006; Dubey et al., 2007). All three tribes are found in North America. Following Dubey et al. (2007), Soricini contains only *Sorex*. Blarinini contains *Blarina*, *Cryptotis*, and one genus not found in North America, *Blarinella*. Notiosoricini is now recognized as a distinct monophyletic group separate from Neomyini, and only includes the sister taxa *Notiosorex* and *Megasorex* (Ohdachi et al., 2006). In the supertree phylogeny of Insectivora constructed by Grenyer and Purvis (2003), Notiosoricini was sister to the clade Soricini + Blarinini. That is the phylogenetic

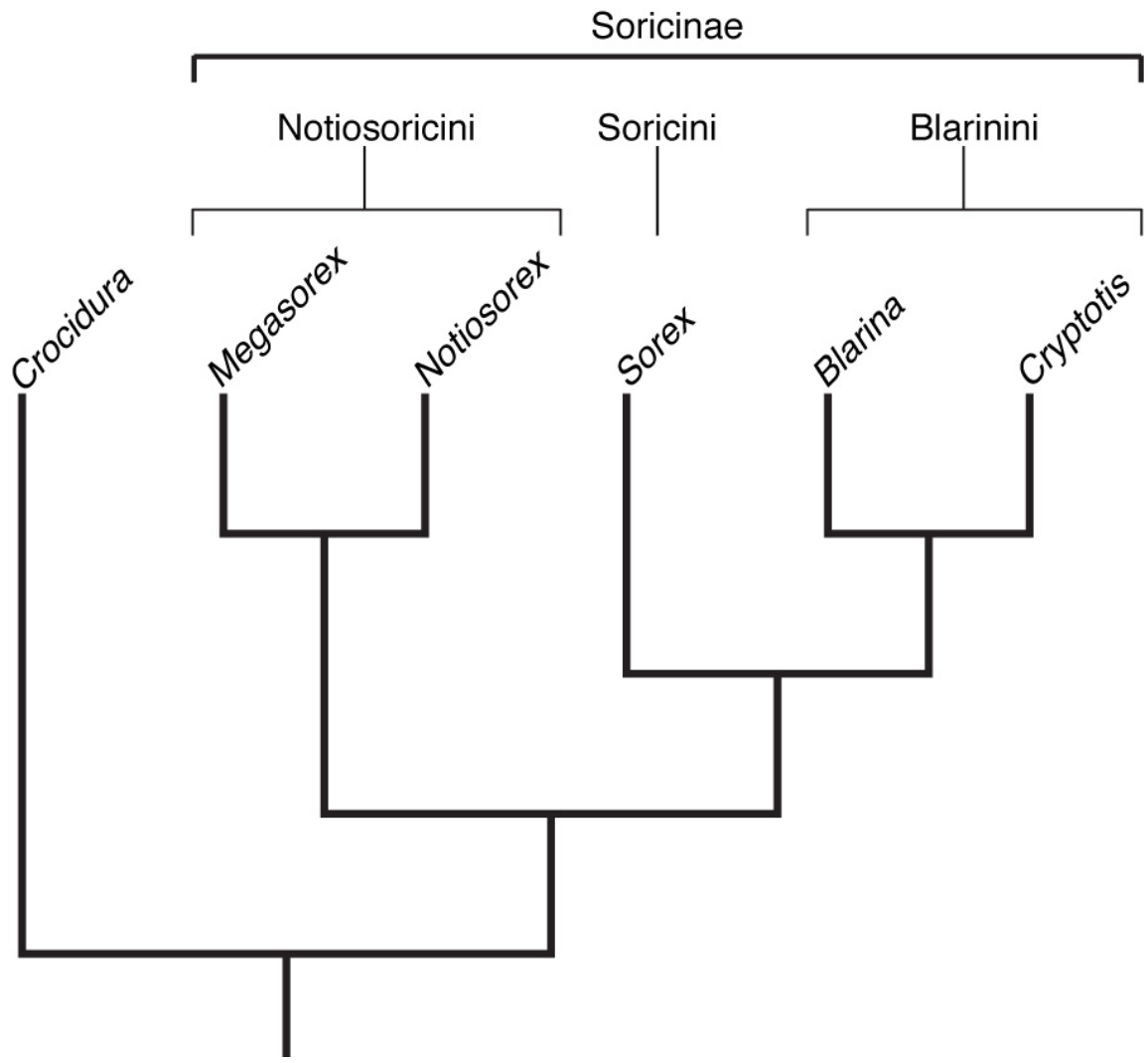


Figure 2.1: The hypothesized relationships of the shrews examined in this study (following Grenyer and Purvis, 2003). *Megasorex*, *Notiosorex,* and *Blarina* are endemic to North America. *Sorex* is Holarctic and Neotropical, and *Cryptotis* is Nearctic and Neotropical in distribution.

hypothesis I will follow throughout this paper (Figure 2.1). I follow this older hypothesis because more recent molecular phylogenies recovered monophyletic tribes, but had the tribes in a polytomy (Ohdachi et al., 2006; Dubey et al., 2007).

Relationships among living species of shrews continue to be refined by mammalogists, as new specimens are collected and newer molecular, morphologic, and morphometric techniques are utilized. The species of *Sorex* and *Cryptotis* are numerous and morphologically similar, and no complete phylogenetic hypothesis has been proposed for either genus. Even the member species are not agreed upon by all authors (Hall, 1981; Wolsan and Hutterer, 1998; Hutterer, 2005).

Megasorex is monotypic and *Notiosorex* was long considered monotypic, but recent revisions based on molecular and morphologic evidence led to the recognition of new species in addition to *Notiosorex crawfordi* (Carraway and Timm, 2000; Baker, O'Neill, and McAliley, 2003; Carraway, 2010). Although, there are now 4 extant and 4 extinct named species of *Notiosorex* there is not a single published phylogenetic hypothesis of this genus. Because the relationships within *Notiosorex* remain unresolved, my focus is on finding characters that differentiate this genus from the other extant North American genera.

The relationship between the three *Blarina* species is well supported, with *Blarina carolinensis* and *Blarina brevicauda* as sister taxa, and *Blarina hylophaga* is sister to them (Brant and Ortí, 2002; Grenyer and Purvis, 2003; Ohdachi et al., 2006). There is the potential to find characters that could differentiate these species.

Identification

The highly specialized and derived dentition of shrews readily sets them apart from other small mammals. All shrew species have greatly enlarged and procumbent lower incisors, large, curved upper incisors, between three to five antemolars of uncertain homology, and three dilambdodont molars. However, the morphologic differences between species are subtle and may be swamped by intraspecific variation. Thus, there are many challenges in identifying shrews to more exclusive taxonomic levels.

Numerous characteristics have been proposed to differentiate shrew species, including cranial and dental morphology, pelage, karyotype, articulated postcranial elements, body mass, and, more recently, genetic data. There are many publications on identification of shrews and their systematic relationships, based upon a variety of molecular and morphologic characters (e.g., George et al., 1982; Dannelid, 1989; Fang et al., 1997; Brant and Ortí, 2002; Woodman et al., 2003). Those studies were focused on particular genera of shrews, which are more common than inclusive studies of multiple taxonomic groups of shrews (e.g., Repenning, 1967; Carraway, 1995; Rofes and Cuenca-Bescós, 2009).

Mammalogists now commonly use morphometric techniques to discriminate species. For example, *Blarina carolinensis* was separated from *Blarina brevicauda* by Genoways and Choate (1972), and two new species of *Notiosorex* were recognized by Carraway and Timm (2000). In both examples, new species of shrews were separated from an existing species with morphometric techniques, such as principle component analysis of linear measurements performed on complete crania. However, the skulls of shrews are delicate compared to other elements and complete skulls are extremely rare for fossil specimens. For example, there are thousands of shrew specimens from Hall's Cave, but not a single cranium is preserved (personal observation). In addition to

fragmentary specimens, many fossilized shrews are found completely disarticulated, even when abundant. Therefore, morphometrics and soft tissue characters are typically unavailable to paleontologists attempting to identify fragmentary bony remains.

The use of apomorphies for the identification of small mammal fossils remains largely unexplored. Previous studies highlighted the limited potential for apomorphies to resolve species identifications in *Microtus* (Bell and Bever, 2006). A recent examination of lagomorphs from Cathedral Cave, Nevada found that when a strict utilization of apomorphies was applied to lagomorphs across a broad geographic distribution many characters used to discriminate species failed (Jass, 2009). The use of geography to restrict the comparison species or specimens is the greatest differentiation between an apomorphic perspective and the traditional means of identifying Quaternary fossils. Often the characters used in to identify taxa in both these schemes are similar if not identical, but their utility as diagnostic characters to discriminate species dissolves when they are compared to a sample of species that encompass a larger geographic or temporal sample, or both.

Given the disparate nature of the samples with which paleontologists and mammalogists work, a common set of criteria for identifying specimens would maximize the ability of both groups to share data and could extend their interpretations over longer time periods and greater geographic areas. Commonly, Quaternary fossil shrew specimens are identified by a comparison of morphologic similarity of the fossil with other fossils or extant specimens from the same region in which the fossils were found (e. g., Klippel and Parmalee, 1982, Toomey, 1993, Schultz, 2010). The use of geographic or temporal assumptions to supplement morphologic similarities to help refine identification of fossil shrews is common for Quaternary-age specimens. This is a hidden assumption that is often not explicitly stated in discussions of how fossils were

identified. Though common, this can lead to a series of potential problems with later interpretations. Fossils that are identified with the aid of geography can impede or eliminate the ability to detect range shifts or temporal extensions.

If assumptions, like assuming that the species found in the same area today were present here in the past, are not made explicit then later workers utilizing the identifications will not be aware that basing their paleoecologic interpretations on those identifications can lead to circular reasoning. Shrews are a common component of Quaternary faunas, and are sometimes used as paleoclimate indicator taxa (e.g., Guilday, 1962; Graham and Semken, 1976; Klippel and Parmalee, 1982; Toomey et al., 1993; van Dam, 2004). Accurate interpretations about paleoclimate based on fossils must be built upon accurate identifications of fossil material. If the identified fossils were only compared to taxa that live in the same area today then it is likely that closely related species from distant geographic regions would not be recognized.

It is essential to have a clear methodological framework to make research reproducible. I will test whether using apomorphic characters will lead to the same level of identification that previous authors reached when they used gross similarity in conjunction with or without geographic assumptions. Identifications based on a diagnosis of discrete apomorphic characters would allow a fossil to be placed within a hierarchy of a given phylogenetic hypothesis. It is reasonable to imagine that technological advancement and continued scholarship will provide greater understanding of biological relationships than is enjoyed today. If fossil specimens are assignable to crown clades, then any additional research on the extant lineage should allow for potentially more robust interpretations of phylogenetic relationships and of the evolution of morphologic characters. In addition, any independent paleoecologic interpretations of a fossil in a phylogeny would enhance the understanding of the evolution of the ecology

of the lineage. This would be a radically different approach to paleoecology because most paleoecological interpretations are based upon our incomplete understanding of the ecology of extant species. A clear understanding of specimen identification will allow other scientists to have a better understanding of the interpretations derived from the data. This way the identifications can be used in a manner consistent with the author's intention, and will reduce the hidden assumptions of identification based (in part) on geography and time.

There is the potential that apomorphic identifications may increase the number of recognized species. This technique has yielded greater taxonomic resolution in Mesozoic faunas (Nesbitt and Stocker, 2008). However there are differences in both the fossil specimens and the techniques used to identify them between Mesozoic and Quaternary faunas. In many cases, fragmentary, isolated Triassic fossils were originally left unidentified or only identified to higher taxonomic clades such as Archosauria (Nesbitt and Stocker, 2008). Many Quaternary small mammals fossils are assumed members of extant genera or species, and there is an expectation that even isolated teeth and jaws can be identified to species by comparing them to specimens of extant taxa. Though Quaternary small mammals are often recovered by screen washing, and identified as elements, by identifying the fossils with robust apomorphies drawn from a geographically diverse comparison pool it is possible that new or different species will be recognized in faunas that were originally identified with narrow geographic assumptions.

In this chapter, I re-examine and reinterpret the cranial and dental characters that were used previously to identify both extinct and extant shrews. My ultimate goal is to establish solid identifications for the tribes and genera of North American shrews to be used to identify Quaternary fossils. The large number of species of *Cryptotis* (30 spp.), *Notiosorex* (8 spp.), and *Sorex* (77 spp.), the disagreement in the number and validity of

species, and the lack of well-supported phylogenies for each of these genera makes it difficult to find reliable apomorphies for species (Hutterer, 2005; Carraway, 2010). At present, only *Blarina* has a well-established phylogeny (Brant and Ortí, 2002; Grenyer and Purvis, 2003; Ohdachi et al., 2006).

I analyzed the cranial and dental characters in a phylogenetic context to explore both how useful these characters are for identifying shrews, and gain a better appreciation of the morphological evolution of shrews. By analyzing characters in a phylogenetic framework I will present explicit characters that will help paleontologists identify shrews in a reproducible manner, and can be further used in phylogenetic hypotheses. I analyzed 40 characters taken from published reports of soricid morphology. I only examined cranial, mandibular, and dental characters because those are the elements most commonly recognized from Quaternary fossil sites. Most of the characters required refining and reinterpretation because they were originally part of dichotomous keys (e.g., Carraway, 1995), or were used to differentiate species within a single genus (e.g., Woodman and Timm, 1999). Several characters were highly modified from their original sources. I provide description and illustration of each character to aid future workers who are interested in both skeletal identifications of shrews and determining the phylogenetic relationships of shrews based on morphology. Each character was assessed for its utility to provide apomorphic identifications. A better understanding of the morphology of the species I examined should lead to improved discussions of character evolution throughout Soricidae.

The second objective of this chapter is to explore the impact of adopting apomorphic characters for the identification of shrews. Establishing a specific methodology for identifying fossils is important because all subsequent interpretations will be based on the taxon name applied to the specimen (Bell et al., 2010). Therefore, I

have provided a complete description of the techniques, assumptions, and alternative interpretations of the identifications of these fossils. Here, I test the difference between apomorphic identification and the traditional approach and examine any potential disparity between these methods on the identification of shrews. My test sample comes from Pit 1E of Hall's Cave. This representative sub-sample covers the latest Holocene through the Pleistocene.

MATERIALS AND METHODS

I examined all extant genera of North American shrews, including all extant species of *Blarina* and *Megasorex*. I chose five species of *Sorex* and four species of *Cryptotis* for this analysis because they were used in phylogenetic analyses and were readily available. These were *Cryptotis goldmani*, *Cryptotis magna*, *Cryptotis mexicana*, *Cryptotis parva*, *Sorex arcticus*, *Sorex bendirii*, *Sorex cinereus*, *Sorex fumeus*, *Sorex trowbridgii*, and *Sorex vagrans*. Those species were among the large number of taxa used previously in molecular analyses and combined morphologic and molecular phylogenies (Grenyer and Purvis, 2003; Ohdachi et al., 2006). Within *Notiosorex*, I included only *Notiosorex crawfordi*.

I chose one species of *Crocidura* (*Crocidura russula*) as the outgroup for this study because *Crocidura* commonly is accepted to be outside of Soricinae and is a member of the subfamily Crocidurinae (Repenning, 1967; Wolsan and Hutterer, 1998; Grenyer and Purvis, 2003; Hutterer, 2005; Ohdachi et al., 2006). *Crocidura* is an extraordinarily speciose genus, so I also examined *Crocidura hirta*, *Crocidura hildegardeae*, *Crocidura mutesae*, and *Crocidura nanilla* to assess a measure of the variation within the outgroup. *Crocidura russula* was scored as 0 for all states that were applicable. A list of the specimens I examined is provided in Appendix A.

I examined characters from published species descriptions, taxonomic keys, and phylogenetic analyses. To create characters that could be used in a phylogenetic analysis, I first examined the expression of the character in the taxon or taxa for which it was originally described, and then examined its inter- and intraspecific variation. For some characters, this led to re-describing the original character, adding or changing character states, or simplifying or deleting states. A description of each character is provided in the Character Description section of the Results.

Morphological characters were scored for each specimen and then compiled for each species (Table 2.1). All observed variation for each species is included in the table. Character states were then traced in MacClade (Maddison and Maddison, 2005) to determine synapomorphies for various clades, as well as autapomorphies of individual taxa. Transformations were examined under delayed transformation (DELTRAN), accelerated transformation (ACCTRAN), and the most parsimonious state.

Though the primary goal for scoring specimens was to trace the characters against existing phylogenetic trees, I took the opportunity to run an analysis in PAUP 4.0b10 (Swofford, 2002). The analysis was run using a branch-and-bound search to ensure that all tree space was examined. All characters were weighted equally. I tested multistate characters as both ordered and unordered.

To explore the impact of apomorphic identification on the identification of Quaternary small mammals I examined the shrews from Pit 1E of Hall's Cave. This is a representative sample of the entire sequence of the cave deposit. The species previously identified from Hall's Cave include *Cryptotis parva*, *Blarina carolinensis*, and *Notiosorex crawfordi*. These three species represent more than 99% of the identified specimens. In addition, I also examined specimens from all the excavation units that were identified as *Sorex*, or a species of *Sorex* because *Sorex* is not present in Texas today and was rare in the

Table 2.1: Taxon list and the states of the characters included in this study. Intraspecific variation is indicated by multiple states per character.

	1	2	3	4	5	6	7	8	9	10
Crocidura russula	0	0	0	?	0	0	0	0	0	0
Blarina brevicauda	1	0&1&2	0&1	0	3	0&1	0&1	1	1	0
Blarina carolinensis	1	0&1&2	0&1&2	0	2&3	0&1	0&1	1	0&1	0
Blarina hylophaga	1&2	0&1&2	0&1&2	0	3	0&1	0	1	0&1	0
Cryptotis goldmani	1	2	1&2	0	1	1	0&1	1	1	1
Cryptotis magna	1&2	1&2	1	0	2	1	1	1	1	1
Cryptotis mexicana	2	1	1&2	0	1&2	1	1	1	1	1
Cryptotis parva	1&2	1&2	1&2	0	2	1	0&1	1	0	0
Megasorex gigas	0	0	0	?	1	0&1	1	0	1	1
Notiosorex crawfordi	3	0&1	0	0	2	0&1	0	0	1	1
Sorex arcticus	2	3	2	1&2	1	1	0	1	1	1
Sorex bendirii	1&2	2	1	0	0	0	0	1	1	0
Sorex cinereus	2	3	2	1&2	0&1	0	0	1	1	1
Sorex fumeus	2	2	2	2	1	0	1	1	1	1
Sorex trowbridgii	2	2	1	0	0	1	1	1	1	1
Sorex vagrans	2	3	2	0	0&1	0&1	0	1	1	1

	11	12	13	14	15	16	17	18	19	20
Crocidura russula	0	0	0	0	0	0	0	0	?	0
Blarina brevicauda	1	1	1	1	0	1	1	1	1	2
Blarina carolinensis	1	0&1	0&1	0&1	0	1	1	1	1	2
Blarina hylophaga	1	0&1	1	1	0	1	1	1	1	2
Cryptotis goldmani	1	1	1	0&1	2	1	0	1	1	2
Cryptotis magna	1	0	1	1	2	0	1	1	1	2
Cryptotis mexicana	1	1	0&1	0	2	1	0	1	1	2
Cryptotis parva	1	0	0&1	0&1	2	0	0	1	1	1
Megasorex gigas	0	1	0&1	1	1	0	2	1	0	1
Notiosorex crawfordi	0	0	0&1	0&1	1	0	2	1	0	1
Sorex arcticus	1	1	0	0	0	1	0	0	2	0
Sorex bendirii	1	1	0	0	0	1	0	0	2	2
Sorex cinereus	1	1	0	0	0	1	0	0	1&2	0
Sorex fumeus	1	1	0	0	0	1	0	0	2	0&2
Sorex trowbridgii	1	1	0	0	0	1	0	0	2	2
Sorex vagrans	1	1	0	0	0	1	0	0	2	2

Table 2.1: continued.

	21	22	23	24	25	26	27	28	29	30
Crocidura russula	0	0	0	0	?	0	0	0	0	0
Blarina brevicauda	1	1	0&1&2	0&1	0&1	0&1	2	1	0&1	1
Blarina carolinensis	1	0&1&2	1&2	1	1	0&1	2	1	0	1
Blarina hylophaga	1	0&1&2	1&2	1	1	0	2	1	0	1
Cryptotis goldmani	2	0	1	1	1	0	1	0&1	1	0&2
Cryptotis magna	2	0&1	1&2	0&1	1	0&1	1	0	0	0&2
Cryptotis mexicana	0	0&1	1&2	0&1	1	1	1	1	1	2
Cryptotis parva	2	0&1	2	0&1	1	0	1	0&1	1	2
Megasorex gigas	0	1&2	0	0	?	1	0	0	0	2
Notiosorex crawfordi	0	1&2	0	0	0&1	0&1	0	0	1	2
Sorex arcticus	0	0	1&2	0	0&1	0	3	0	0	2
Sorex bendirii	0	0	0	0	0	0	3	0	1	2
Sorex cinereus	0	0	0	0	1	0	3	0	0&1	0&2
Sorex fumeus	0	0	2	0	0	0&1	3	0	0	2
Sorex trowbridgii	0	0	1	1	1	0	3	0	1	2
Sorex vagrans	0	0&1	2	0	1	0	3	0	1	2

	31	32	33	34	35	36	37	38	39	40
Crocidura russula	0	0	0	0	0	0	0	0	0	0
Blarina brevicauda	0&1	1	0	0&1	0	3	2	0	0	3
Blarina carolinensis	1	1	0	0	0	3	0	0	0	1
Blarina hylophaga	0&1	1	0	0&1	0	3	2	0	0	3
Cryptotis goldmani	0&1	0&1	0	0&1	1	2	3	1	1	3
Cryptotis magna	0	1	0	0	1	2	2	0&1	1	3
Cryptotis mexicana	1	1	0&1	0	1	2	3	1	1	3
Cryptotis parva	0&1	0	0&1	0	0	1	0	0	0	1
Megasorex gigas	1	0&1	1	1	2	?	1	0	0	2
Notiosorex crawfordi	0&1	0	1	0	2	?	1	0	0	2
Sorex arcticus	1	0	0&1	1	1	2	3	0&1	0	0
Sorex bendirii	1	0	1	1	0	2	3	1	0	0
Sorex cinereus	1	0	0&1	1	1	1&2	0&3	0	0	0
Sorex fumeus	1	0	0&1	1	1	1	0	0	0	0&2
Sorex trowbridgii	1	0	0	1	1	1	0	0	0	1
Sorex vagrans	1	0	0&1	1	1	1	0	0	0	0

Quaternary. These were identified as *Sorex cinereus*, *Sorex* cf. *haydeni*, and *Sorex cinereus* or *haydeni* [sic] (Toomey, 1993). Pit 1E was combined with Pit 1D from 160 cm to 240 cm depth (Toomey, 1993). Specimens from the combined levels were examined as well. This large sample of shrews covers the full diversity of species that were originally identified, and includes the various states of preservation found in the cave deposit.

RESULTS

The 40 characters I examined are discussed below with a description of each state (Table 2.2). With each character description, I include the citations of papers where the character was proposed or discussed, and the number of the character as listed in each publication.

Character Descriptions

Pigmentation

Character 1: Teeth pigmentation; 0 = no pigment, 1 = heavy, 2 = moderate, 3 = light; Figure 2.2 (Carraway, 2007, 1; Rofes and Cuenca-Bescós, 2009, 1).

The character states described by Carraway (2007) and Rofes and Cuenca-Bescós (2009) were restricted to presence or absence of pigment. However, Carraway illustrated pigment variation between the four genera of Mexican shrews. All North American shrews belong to Soricinae, which are the 'red-toothed' shrews, but there is a wide range of pigmentation. Other authors utilized the variation in pigmentation to differentiate North American shrew genera in descriptions and keys (Repenning, 1967; Jones and Manning, 1992).

Table 2.2: Characters and states.

	Character	State 0	State 1	State 2	State 3
1	Teeth pigmentation	0 = no pigment	1 = heavy	2 = moderate	3 = light
2	Denticulations on lower incisor (i1)	0 = absent	1 = one present	2 = two present	3 = three or more
3	Interdenticular space	0 = absent	1 = shallow	2 = deep	
4	Pigment on i1	0 = one segment	1 = two segments	2 = three segments	
5	Posterior extent of alveolus of i1 in labial view	0 = mesial half of p4	1 = distal end of p4 to paraconid of m1	2 = past paraconid to metaconid of m1	3 = past metaconid of m1
6	Labial cingulum on i1	0 = absent	1 = present		
7	Upturning of distal tip of i1	0 = strong	1 = slight		
8	2nd cusp on p4 in labial view	0 = absent	1 = present		
9	Talonid of m1 and m2	0 = anteroposteriorly reduced relative to trigonid	1 = equivalent in size to trigonid		
10	Ridge between entoconid and protoconid on m1	0 = absent	1 = present		
11	Pigmentation on m2, m3	0 = absent	1 = present		
12	Cusps on talonid of m3	0 = one cusp on talonid (hypoconid)	1 = two (both hypoconid and entoconid)		
13	Coronoid spicule	0 = slight	1 = robust		
14	Size of coronoid processes relative to height	0 = narrow	1 = wide		
15	Angle of the coronoid process from the horizontal ramus	0 = perpendicular	1 = leans forward	2 = leans backward	
16	Excavated area on lingual side of posterior dentary, ventral to condyle	0 = present	1 = absent		
17	Ventral contact of condyle to sigmoid notch	0 = condyle separate from sigmoid notch	1 = no separation from sigmoid notch	2 = groove between condyle and sigmoid notch	
18	Length of angular process	0 = long, extending past condyle in lateral view	1 = shorter than condyle, or slightly longer		

Table 2.2: continued.

	Character	State 0	State 1	State 2	State 3
19	Interarticular condyle area	0 = emarginated area between condyles, area between condyles much narrower than condyles	1 = slightly emarginated area between condyles, lower condyle extremely broad	2 = little emargination between condyles, area between condyles approximately equal in width to condyles	
20	Articular condyle in labial view	0 = short upper condyle and short overall length of condyle	1 = short upper condyle and lower condyle distinct in lateral view	2 = long upper condyle and lower condyle slight or absent from lateral view	
21	Lingual side of interarticular area	0 = no basin	1 = wide basin	2 = slight basin	
22	Internal temporal fossa	0 = large	1= medium	2 = small	
23	Canal into temporal fossa	0 = absent	1 = present, well-developed	2 = tiny hole	
24	Mandibular canal	0 = separate from temporal fossa	1 = close to/connecting to canal into temporal fossa		
25	Pigment on I1	0 = tip of I1 and posterior cusplet	1 = all over		
26	I1 alveolus orientation in lateral view	0 = vertical	1 = angled down		
27	Number of antemolars per upper jaw	0 = three	1 = four	2 = four visible in lateral view (five present)	3 = five visible in lateral view
28	Conical cusp on antemolars	0 = absent	1 = present		
29	Broad antemolars	0 = present	1 = absent		
30	Relative size of antemolars	0 = large 1st antemolar	1= large 2nd antemolar (taller than A1)	2 = 1st two antemolars equal in size	
31	Protoconal basin of M1	0 = smaller than hypoconal basin	1 = equal to or larger than hypoconal basin		
32	Posterior border of P4, M1, and M2	0 = strong emargination	1 = slight to no emargination		
33	Shape of M2	0 = trapezoidal	1 = rectangular		
34	M3 cusp morphology	0 = simplified	1 = well developed		
35	Zygomatic process of maxillary	0 = originates opposite mesostyle of M2	1 = to posterior part of M2	2 = absent	

Table 2.2: continued.

	Character	State 0	State 1	State 2	State 3
36	Posterior extent of zygomatic process in ventral view	0 = not past M2	1 = middle of M3	2 = to end of M3 or past	3 = to M3
37	Shape of zygomatic process	0 = short	1 = absent	2 = wide	3 = long
38	Zygomatic process extends below occlusal surface in lateral view	0 = absent	1 = present		
39	Location of anterior end of zygomatic plate	0 = in line with the mesostyle M1	1 = in between M1 and M2		
40	Location of posterior end of zygomatic plate	0 = anterior to mesostyle M2	1 = even with or anterior to the anterior extent of the zygomatic process	2 = posterior to M2	3 = posterior to M2 and confluent with posterior base of the zygomatic process

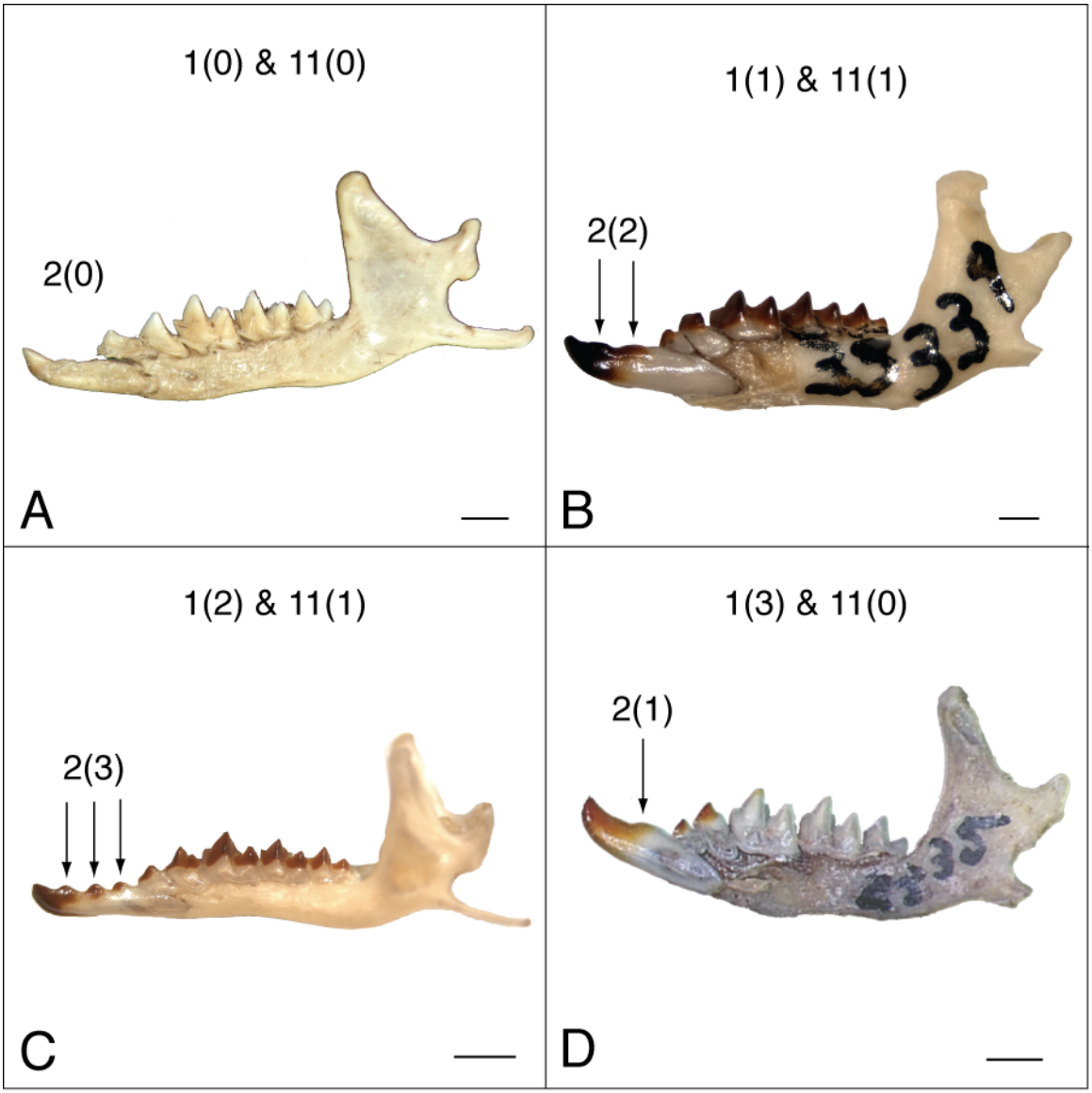


Figure 2.2: Left dentaries showing character 1, teeth pigmentation, and character 2, denticulations on lower incisor, and character 11, pigment on m3. A. *Crocidura russula* (TMM M-4130) B. *Blarina carolinensis* (TCWC 33339) C. *Sorex cinereus* (TCWC 26977) D. *Notiosorex crawfordi* (TCWC 2335). See text for state descriptions. Scale bar = 1 mm.

I observed individual variation in the degree of teeth pigmentation, possibly due to age, diet, or environment. Each species showed some level of variation, with the exception of the unpigmented species (Fig. 2.2A). I observed that the darkest pigment is most consistently found in the teeth of *Blarina.* Those teeth will grade in color from red to nearly black at the tips of the molars. This corresponds to state 1, heavy pigmentation (Fig. 2.2B). *Cryptotis* may have dark red to black tips on i1, however the molars remain reddish. It is the black tips on the molars that set *Blarina* teeth apart from the other genera. Some specimens of *Cryptotis* were almost as dark, with black tips on i1 and extremely dark red molars. *Cryptotis* and *Sorex* have red, moderately dark pigmentation. This corresponds to state 2, moderate pigmentation (Fig. 2.2C). The degree of pigmentation in *Cryptotis* and *Sorex* is typically intermediate between *Blarina* and *Notiosorex*. *Notiosorex* has light pigmentation that is orange to tan (Fig. 2.2D). *Megasorex* is the only North American shrew without pigment. This plesiomorphic state makes it readily recognizable only when compared to other extant North American taxa. All specimens of *Crocidura* I examined also lacked pigment.

Lower Dentition

Character 2: Number of denticulations on lower incisor (i1); 0 = absent, 1 = one present, 2 = two present, 3 = three or more present; Figure 2.2 (Carraway, 1995, 2007, 18).

Denticulations are a series of bumps on the anterior surface of the large procumbent lower incisor. The denticulations are subject to significant wear through

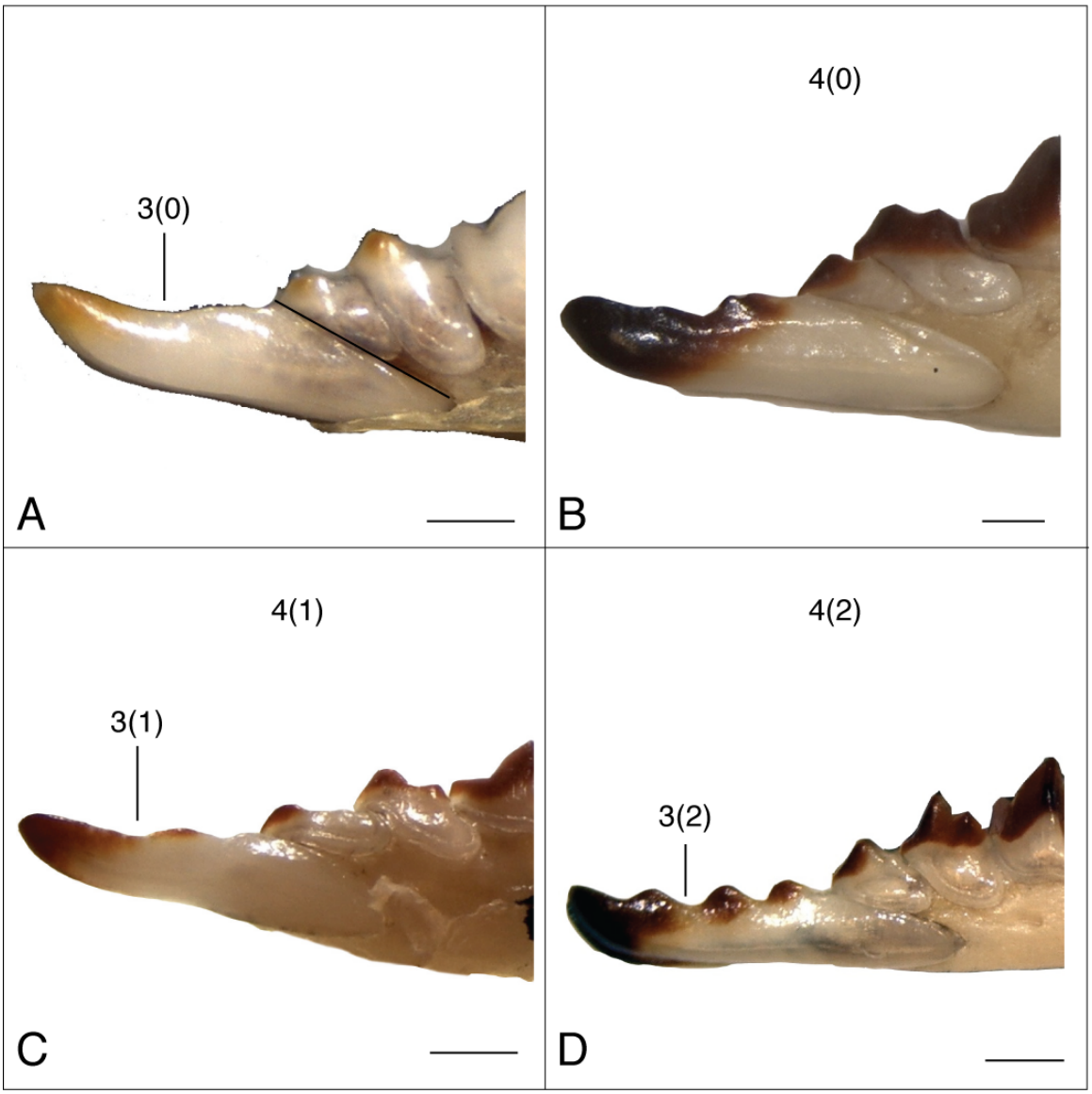


Figure 2.3: Lower left incisors (i1) showing character 3, interdenitcular space and character 4, number of pigment areas on i1. A. *Notiosorex crawfordi* (TCWC 2335) B. *Blarina carolinensis* (TCWC 33339) C. *Sorex trowbridgii* (TCWC 45855) D. *Sorex cinereus* (TCWC 26977). Scale bar = 0.5 mm.

ontogeny. The character is less informative in older individuals because the denticulations are often worn away (Pearson, 1945). The observed number of denticulations varied from zero to three. This character was used in a key to separate *Sorex hoyi* from other North American soricids (Carraway, 1995, step 2). The expression of this character was not fully explored by Carraway because the key was only for recent shrews of the western United States and Canada. I found that it was polymorphic in *Cryptotis magna, Cryptotis parva, Notiosorex crawfordi*, and all species of *Blarina*.

Character 3: Interdenticular space; 0 = absent, 1 = shallow, 2 = deep; Figure 2.3 (Carraway, 2007, 19).

This character is a relative measure of the height of denticulations on i1. This character was divided into three states (shallow, moderate, and deep) by Carraway (2007). I found that the differences in the height of the denticulations were too subtle to allow for a moderate state. I retained only deep and shallow because it was simpler and less ambiguous to divide the depth of the denticulations into those categories. I scored the interdenticular space as shallow when there was subtle depression between denticulations (Fig. 2.3C). Where denticulations were distinct and were at least 0.25 mm high I scored the interdenticular space as deep (Fig. 2.3D). Specimens without denticulations were scored as absent for this condition (Fig. 2.3A).

As described in character 2, the denticulations are highly susceptible to wear. Shrews can be put into age classes using molar wear (Pearson, 1945), but exact ages are

difficult to determine in such short-lived mammals (Pruitt, 1954). I examine the problem of ontogenetic wear in shrew teeth in the discussion. I observed many specimens where denticulations were worn down to a shallow or almost absent condition, but were possibly deep in a younger individual. They were scored as they appeared.

Character 4: Pigment on i1; 0 = 1 segment, 1 = 2 segments, 2 = 3 segments; Figure 2.3 (Carraway, 1995, 2007, 20).

Most shrews have one contiguous area of pigment on i1. This character was not scored for taxa that lack pigment (*Crocidura russula* and *Megasorex*) so as not to unnecessarily homologize the absence of pigment. I determined one segment to be the primitive state because it is found in *Notiosorex crawfordi* and in all *Blarina* and *Cryptotis* (Fig. 2.3B). This character was used to separate *Sorex* species by Carraway (1995, 2007). In *Sorex*, areas of pigment may appear as isolated patches on one or two of the denticulations. Not all species of *Sorex* show this; however, among North American taxa more than one segment of pigment only occurs within some specimens of *Sorex*. *Sorex cinereus*, *Sorex fumeus,* and *Sorex arcticus* had three pigment segments (Fig. 2.3D), and in some specimens *Sorex cinereus* and *Sorex arcticus* also had two segments of pigment (Fig. 2.3C).

Character 5: Posterior extent of i1 in labial view; 0 = under mesial half of p4, 1 = from distal end of p4 to paraconid of m1, 2 = past paraconid but not past metaconid of m1, 3 = past metaconid of m1; Fig. 2.4 (derived from Carraway, 2007, 16).

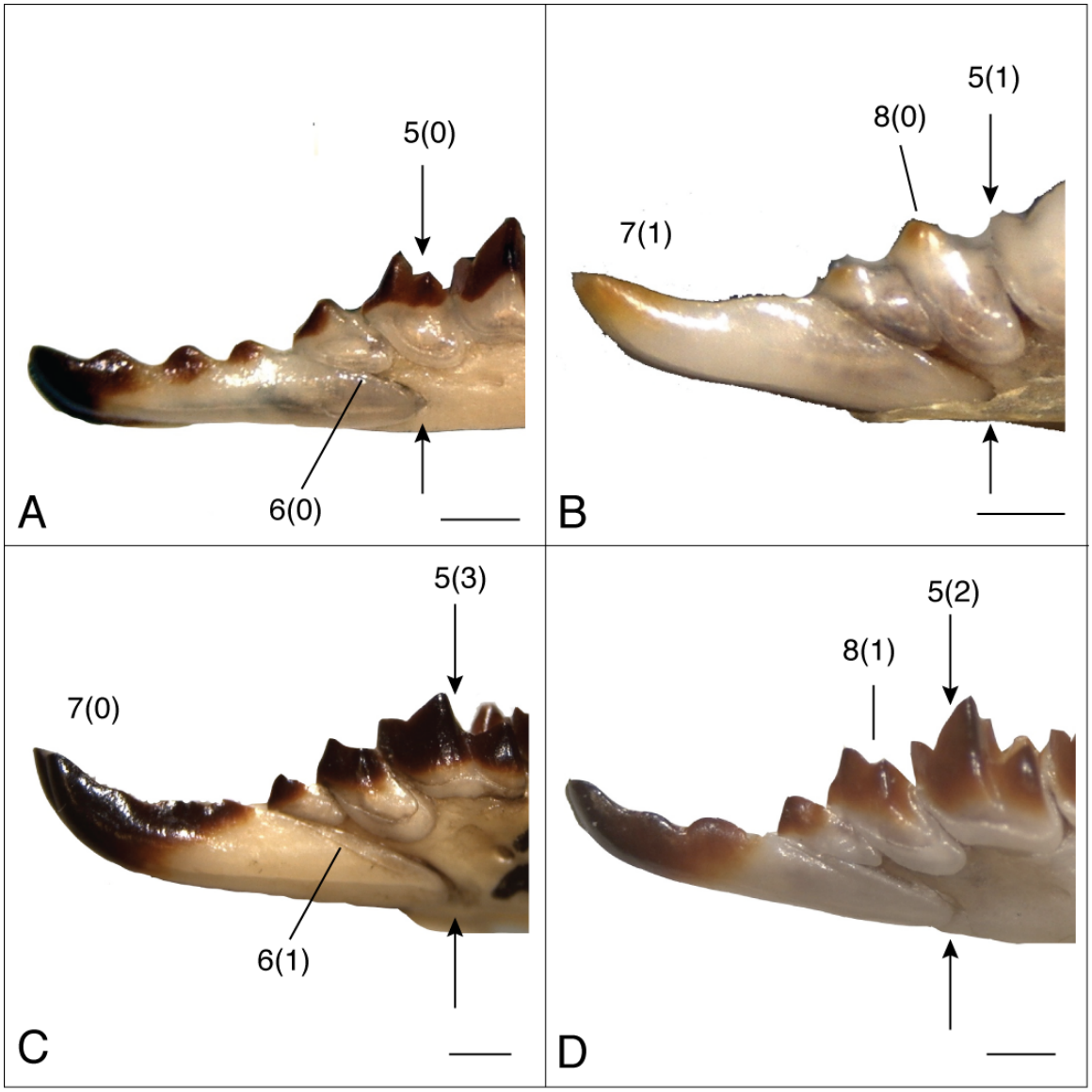


Figure 2.4: Lower incisor (i1) through fourth premolar (p4) showing characters 5, 6, 7, and 8. The arrows show the alignment of character 5; lower arrow points to the posterior of i1 and the upper arrow to the cusp on p4 or m1 under which it sits. A. *Sorex cinereus* (TCWC 26977) B. *Notiosorex crawfordi* (TCWC 2335) C. *Blarina brevicauda* (TCWC 23684) D. *Cryptotis parva* (TCWC 45855) Scale bar = 0.5 mm.

This character is scored for the furthest posterior extent of the alveolus of i1 in labial view. The unusual orientation of the procumbent lower incisor of shrews allows the alveolus to extend under the p3, p4, and in some cases past the metaconid of m1. This character was described by Carraway (1995, 2007) as extending posteriorly beneath paraconid of m1, or not. This characteristic separated *Sorex hoyi* from other *Sorex* and all other North American shrews (Carraway, 1995). I observed consistent variation of the distal extent of i1 between taxa, so I created four states for this character.

State 0 was found in *Crocidura russula* and several species of *Sorex* (Fig. 2.4A). Some species of *Sorex* had state 1 (Fig. 2.4B), and *Sorex cinereus* and *Sorex vagrans* varied between 0 and 1. *Blarina* consistently had state 3 (Fig. 2.4C). The exception to this was *Blarina carolinensis*; it varied between states 2 and 3 (Fig. 2.4D and C).

Character 6: labial cingulum on i1; 0 = absent, 1 = present; Fig. 2.4 (Rofes and Cuenca-Bescós, 2009, 15).

This character is simply the presence or absence of a cingulum on i1. Twelve cingulum characters were used by Rofes and Cuenca-Bescós (2009). There was no description of any of their characters beyond present or absent. The cingulum on i1 was subtle, but varied less between specimens of the same species than cingula on the other teeth. I interpreted this character as the absence (Fig. 2.4A) or presence (Fig. 2.4A) of a slightly raised band on the tooth immediately adjacent to the alveolus. This character

was polymorphic in *Blarina*, *Sorex vagrans,* and the Notiosoricini, but constant in the other taxa.

Character 7: Upturning of distal tip of i1; 0 = strong, 1 = slight; Fig. 2.4 (Rofes and Cuenca-Bescós, 2009, 16).

This character is polymorphic and seems to be easily affected by wear. *Sorex* was scored by Rofes and Cuenca-Bescós (2009) as state 0 (slight). Their primitive character states were based on *Sorex*, specifically *Sorex minutus*, *Sorex bor*, and *Sorex praearaneus*. They scored their characters from fossil Eurasian shrews so it is possible that the tips of i1 in their specimens were worn. Contrary to this, I found that most of the *Sorex* species I examined showed a strong upturning of the i1 (Fig. 2.4C). Only *Sorex cinereus* and *Sorex trowbridgii* showed slight upturning (Fig. 2.4B).

Character 8: Second cusp on p4 in labial view; 0 = absent, 1 = present; Fig. 2.4.

This is a new character. In the Notiosoricini, the p4 is simple, conical, and without a secondary cusp (Fig. 2.4B). The Soricini and Blarina have a larger and more complex p4 that has a second cusp. The p4 may appear to have two distinct cusps in labial view (Fig. 2.4D). In other cases the p4 will have a main cusp, and the secondary cusp will appear only as a wide extension posterior to the main cusp. That condition was scored as present.

Character 9: Talonid of m1 and m2; 0 = anteroposteriorly reduced relative to trigonid, 1 = equivalent in size to trigonid; Fig. 2.5 (Repenning, 1967).

This character represents a comparison of whether or not the talonid is close to the same length as the trigonid in m1 and m2 or if it is considerably shorter. I scored this character as state 0 when the talonid was approximately half the length of the trigonid (Fig. 2.5A). This character was used by Repenning to differentiate *Blarina* from the other Blarinini. When Repenning wrote his monograph one extant species of *Blarina* was recognized. I found that this character varied within *Blarina*. Both *Blarina carolinensis* and *Blarina hylophaga* had both states, but *Blarina brevicauda* only had state 1 (Fig. 2.5B). In addition, I found that *Cryptotis parva* had state 0. My observations are inconsistent with Repenning's findings that only *Blarina* had a reduced talonid.

Repenning reported that the genus *Blarina* showed greater variation than any other extant genus he examined (Repenning, 1967). This concurs with my overall findings that *Blarina* had the most intraspecific variation of all the taxa I examined.

Character 10: Ridge between entoconid and metaconid (entocristid) on m1; 0 = absent, 1 = present; Fig. 2.5 (Rofes and Cuenca-Bescós, 2009, 26, 27).

On the lingual side of m1, the entocristid, a small ridge that connects the entoconid to the protoconid, may be present. That structure was referred to as the entoconid crest by Repenning (1967) and Rofes and Cuenca-Bescós (2009). The character was scored by Rofes and Cuenca-Bescós (2009) as both the presence/absence

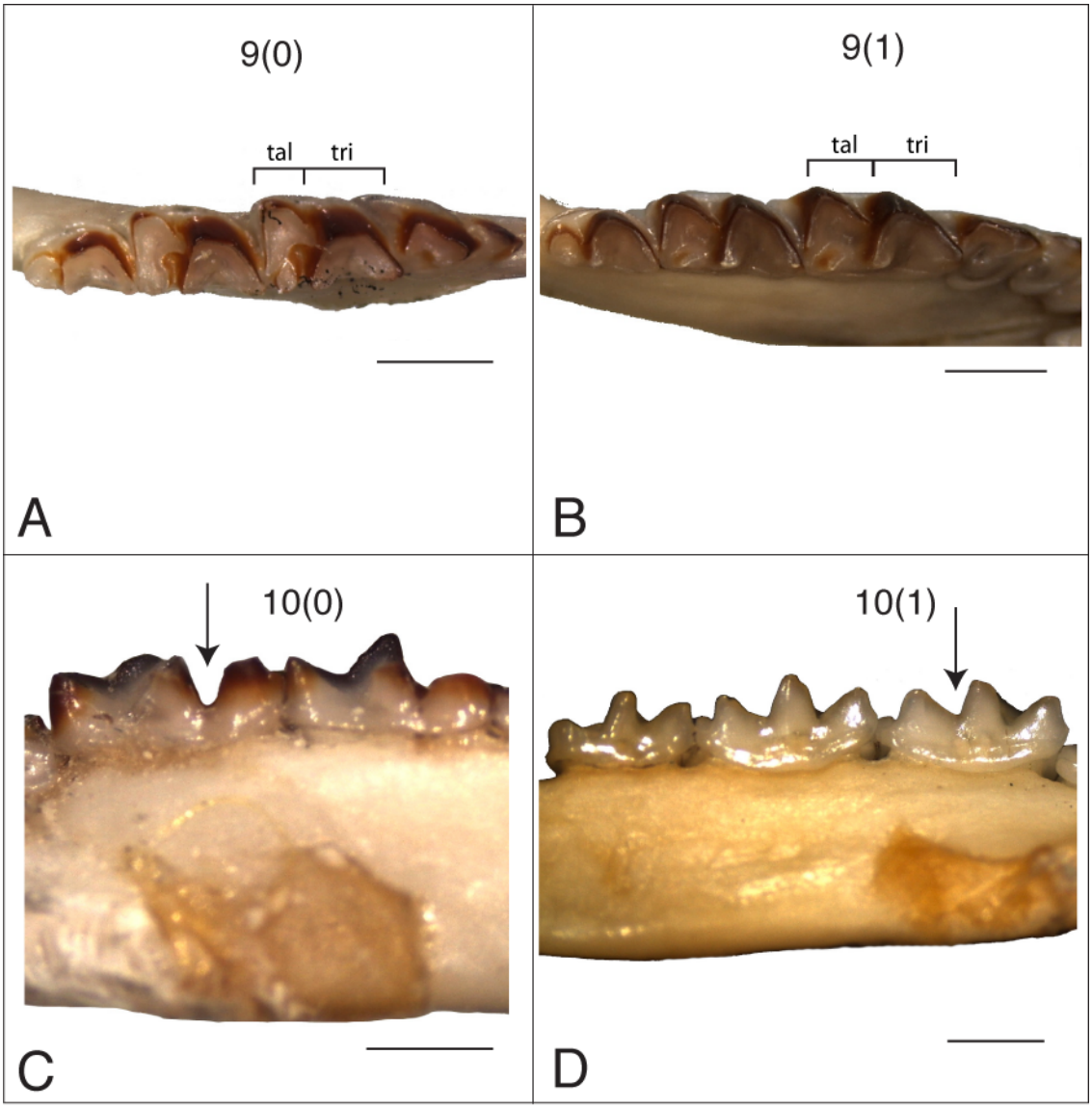


Figure 2.5: Characters 9 and 10. The lines in A and B show the relative size of the talonid (tal) and trigonid (tri). The arrows in C and D indicate the area between the entoconid and metaconid. A. *Cryptotis parva* (TCWC 50182) B. *Cryptotis magna* (TCWC 41952) C. *Blarina carolinensis* (TCWC 33359) right lower teeth D. *Megasorex gigas* (TCWC 5829) left lower teeth. Scale bar = 1 mm.

of the ridge (their character 26) and whether it was high or low (their character 27). I did not discriminate any difference in height of the ridge; I only scored it as present or absent. The character was scored as present in *Sorex* (Fig. 2.5D) by Rofes and Cuenca-Bescós (2009). My results agree, except it was absent in *Sorex bendirii* (Fig. 2.5C).

Character 11: Pigmentation on m2 and m3; 0 = absent, 1 = present; Fig. 2.2 (modified from Carraway, 1995).

This character was used by Carraway (1995) to separate *Notiosorex crawfordi* from other North American shrews. *Megasorex gigas* was not included in her key. I observed no intraspecific variation for this character. It is absent in *Notiosorex crawfordi*, *Megasorex gigas*, and *Crocidura russula* (Fig. 2.1A/D), but present in all other taxa I examined (Fig. 2.1B/C).

Character 12: Cusps on talonid of m3; 0 = One (hypoconid), 1 = Two (both hypoconid and entoconid); Fig. 2.6 (Woodman and Timm, 1999, 2003, 25; Rofes and Cuenca-Bescós, 2009, 29).

This character was written the same as character 29 by Rofes and Cuenca-Bescós (2009) but the states were reversed in their character, with two cusps primitive and one derived. This was a difficult character to score primarily because cusp morphology is highly susceptible to wear. The hypoconid and entoconid are small cusps in most taxa.

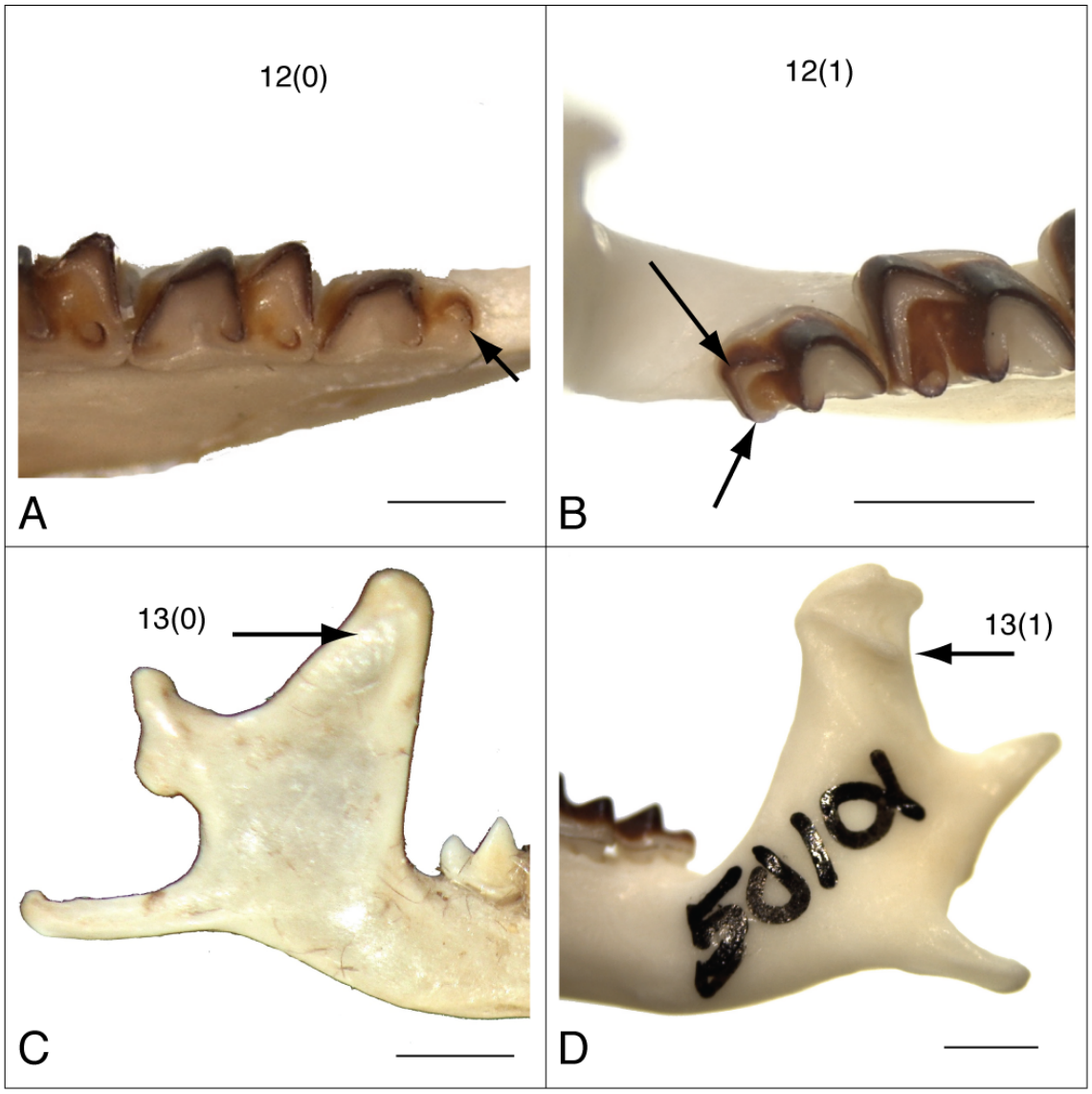


Figure 2.6: Character 12, cusps on talonid of m3. Arrows point to cusps on m3 in A and B. Character 13, coronoid spicule. Arrows point to the coronoid spicule in C and D. A. *Cryptotis parva* (TCWC 50181) B. and D. *Blarina brevicauda* (TCWC 50101) C. *Crocidura russula* (TMM M-4130). Scale bar = 1 mm.

Even slight wear made it difficult to determine whether both cusps were present. The polymorphism inherent to this character was suggested by Woodman and Timm (1999) in their character states. Their scoring was 'entoconid of m3: well developed, present in > 75% of specimens (0); vestigial, but present in < 76% of specimens (1); absent (2).' They later modified the percentages to 'entoconid of m3: well developed, present in > 90% of specimens (0); vestigial, but present in < 50% of specimens (1); absent in > 80% of specimens (2)' (Woodman and Timm, 2003). I observed polymorphism in number of cusps in *Blarina carolinensis* and *Blarina hylophaga*.

Dentary

Character 13: Coronoid spicule; 0 = slight; 1 = robust; Fig. 2.6 (Carraway, 1995; Rofes and Cuenca-Bescós, 2009, 38, 39).

This character describes the size of the coronoid spicule. Two characters for this structure were used by Rofes and Cuenca-Bescós (2009). States of their character 38 are 'small' or 'large' and for their character 39 states were 'weak' or 'pronounced.' These seemed redundant to me so I only used one character to describe this morphology. This character was used by Carraway (1995) to separate *Cryptotis parva* from *Blarina*. The two conditions in the key were 'moderately low' for *Cryptotis parva*, and 'large, usually extending beyond posterior edge of coronoid process in lingual view' for *Blarina* (Carraway, 1995:6). Those descriptions were too complex to score accurately, so I simplified the description of the states. I observed some differences in the shape, angle,

and size of the coronoid process but I could not codify the differences into consistent characters.

I found that *Cryptotis parva, Cryptotis mexicana,* and *Blarina carolinensis* showed both slight and robust coronoid spicules. *Cryptotis magna, Cryptotis goldmani,* and the other species of *Blarina* had robust coronoid spicules (Fig. 2.6D). Therefore, this character does not work to separate *Cryptotis* from *Blarina* as used by Carraway (1995). *Megasorex gigas* and *Notiosorex crawfordi* also had both slight and robust coronoid spicules. *Sorex* had the slightest spicules (Fig. 2.6C).

Character 14: Tip of coronoid processes relative to base; 0 = narrow, 1 = wide; Fig. 2.7 (Carraway, 2007, 22; Rofes and Cuenca-Bescós, 2009, 35).

This character was described by Carraway (2007) as 'size of coronoid processes relative to height—slender or broad' and by Rofes and Cuenca-Bescós (2009) as 'coronoid process apex: (0) narrow; (1) wide.' I phrased this character to describe that in some shrews the coronoid process narrows towards the end, whereas in others it has the same width from the base to the end of the process.

A wide coronoid process is common among the larger species. It is found in all species of *Blarina*, *Megasorex gigas*, and *Cryptotis magna* (Fig. 2.7B). The smaller shrews tend to have a narrow coronoid process (Fig. 2.7A), with the exception of *Cryptotis goldmani, Cryptotis parva,* and *Notiosorex crawfordi*. Those species are polymorphic for this character, as is *Blarina carolinensis*.

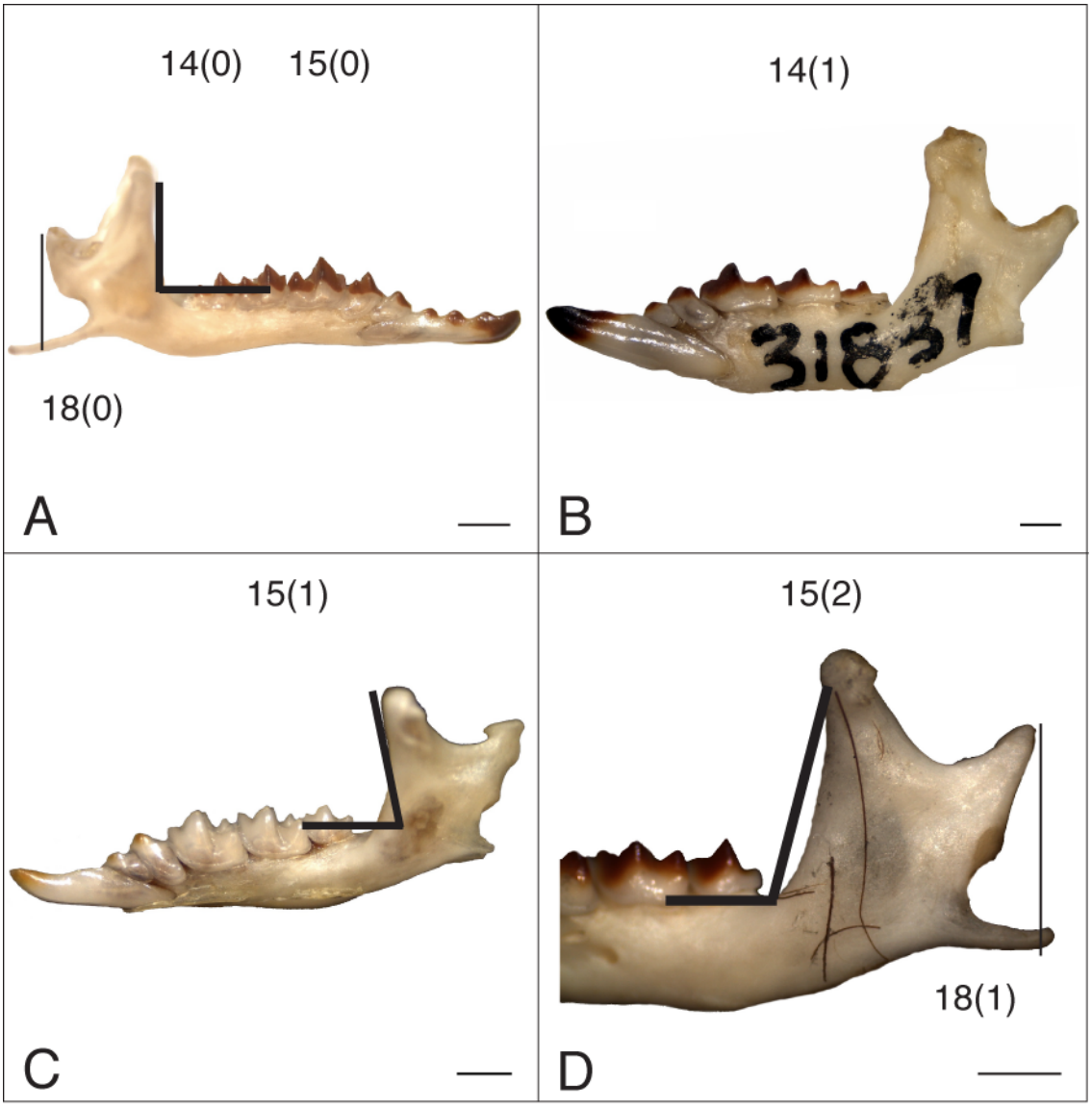


Figure 2.7: Characters 14, 15 and 18. A. *Sorex cinereus* (TCWC 26977) B. *Blarina hylophaga* (TCWC 31837) C. *Notiosorex crawfordi* (TTU 9728) D. *Cryptotis parva* (TCWC 50180). See text for description of character states. Scale bar = 1mm.

Character 15: Angle of the coronoid process as measured from the anterior edge of the process to the horizontal ramus; 0 = perpendicular, 1 = leans forward, 2 = leans backward; Fig. 2.7 (Woodman and Timm, 1999, 2003, 6; Carraway, 2007, 21; Rofes and Cuenca-Bescós, 2009, 36, 37).

The character states were described as 'straight or tipped anteriorly relative to horizontal plane of mandible' by Carraway (2007). The character states used by Woodman and Timm (1999, 2003) were 'anterior border of coronoid process: steep, forming a narrow angle with horizontal ramus of mandible (0); less steep, forming a wide angle with horizontal ramus of mandible (1).' This angle was described in two characters by Rofes and Cuenca-Bescós (2009); first as leaning forward or straight (36) and second as slight or strong (37).

The expression of this character is quite subtle, and would be difficult to quantify. Another challenge to scoring this character is that the coronoid processes in some specimens tend to flare laterally away from the vertical plane of the dentary. *Crocidura russula*, *Blarina,* and *Sorex* all were scored as having perpendicular (0) coronoid processes (Fig. 2.7A). This means that the anterior edge of the coronoid process near its apex is essentially perpendicular to the horizontal ramus. My results differ from the results of Rofes and Cuenca-Bescós (2009); they scored *Sorex* as leaning forward. In *Megasorex gigas* and *Notiosorex crawfordi*, the anterior edge of the coronoid process appears to be anteriorly tilted, or curved forward (Fig. 2.7C). The anterior edge of the apex of the coronoid process in these taxa is at least even with the base of the process. All *Cryptotis*

species show the opposite state, where the anterior edge of the coronoid process forms an obtuse angle with the horizontal ramus (Fig. 2.7D). None of the specimens I examined had a coronoid process that leaned strongly forward or back.

Character 16: Excavated area on lingual side of posterior dentary, ventral to condyle; 0 = present, 1 = absent; Fig. 2.8.

This character and character 17 describe the morphology of the posterior portion of the lingual side of the dentary. There is a complex association between the condyles, the lower part of the dentary, and the angular process. *Crocidura russula, Cryptotis magna, Cryptotis parva, Megasorex gigas,* and *Notiosorex crawfordi* have a deeply incised area on the lingual side of the dentary, ventral to the condyle (Fig. 2.8A). The bone thins greatly and makes a sharp edge in the area between the condyle and the angular process. There was no intraspecific variation. In other taxa, the bone remains thicker and the angular processes round in cross-section rather than partially excavated like the dentary (Fig. 2.8D).

Character 17: Ventral contact of condyle to sigmoid notch; 0 = condyle separate from sigmoid notch, 1 = no separation from sigmoid notch, 2 = groove between condyle and sigmoid notch; Fig. 2.8.

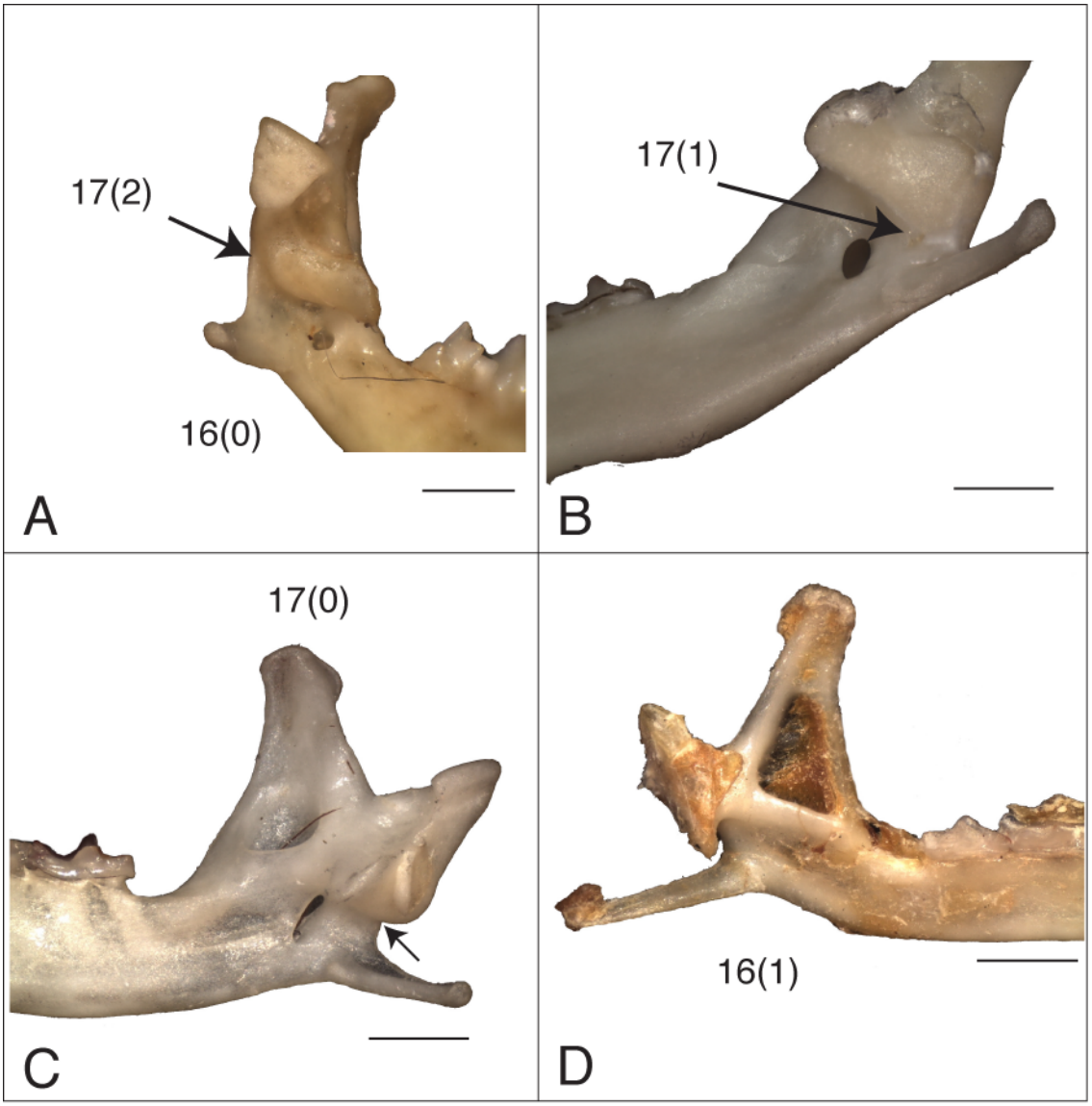


Figure 2.8: Character 16, excavated area on lingual side of the dentary and character 17, ventral contact of condyle to sigmoid notch. Arrows point to the contact point between the condyle and the dentary. A. *Notiosorex crawfordi* (TTU 92929) B. *Blarina carolinensis* (TCWC 333359) C. *Cryptotis parva* (TCWC 50182) D. *Sorex cinereus* (TCWC 20642). Scale bar = 1 mm.

I devised this character to describe the morphology of how the condyle contacts the sigmoid notch. The ventral articular condyle in all *Sorex*, *Cryptotis mexicana*, and *Cryptotis parva* is distinctly separate from the sigmoid notch (Fig. 2.8C). In all *Blarina* and *Cryptotis magna*, the ventral condyle is smoothly connected to the dentary (Fig. 2.8B). There is a narrow groove that separates the condyle and the sigmoid notch in *Megasorex gigas* and *Notiosorex crawfordi* (Fig. 2.8A).

Character 18: Length of angular process; 0 = long, extending past condyle in lateral view, 1 = shorter than condyle, or slightly longer; Fig. 2.7.

I did not find any other author who used the angular process as either a phylogenetic character or a character within a key. *Sorex* species have the longest angular processes observed among these taxa (Fig. 2.7A). All other taxa except *Crocidura russula* have short processes (Fig. 2.7D).

Character 19: Interarticular condyle area; 0 = emarginated area between condyles, area between condyles much narrower than condyles, 1 = slightly emarginated area between condyles, lower condyle extremely broad, 2 = little emargination between condyles, area between condyles approximately equal in width to condyles; Fig. 2.9 (modified from Repenning, 1967, Carraway, 1995, 2007).

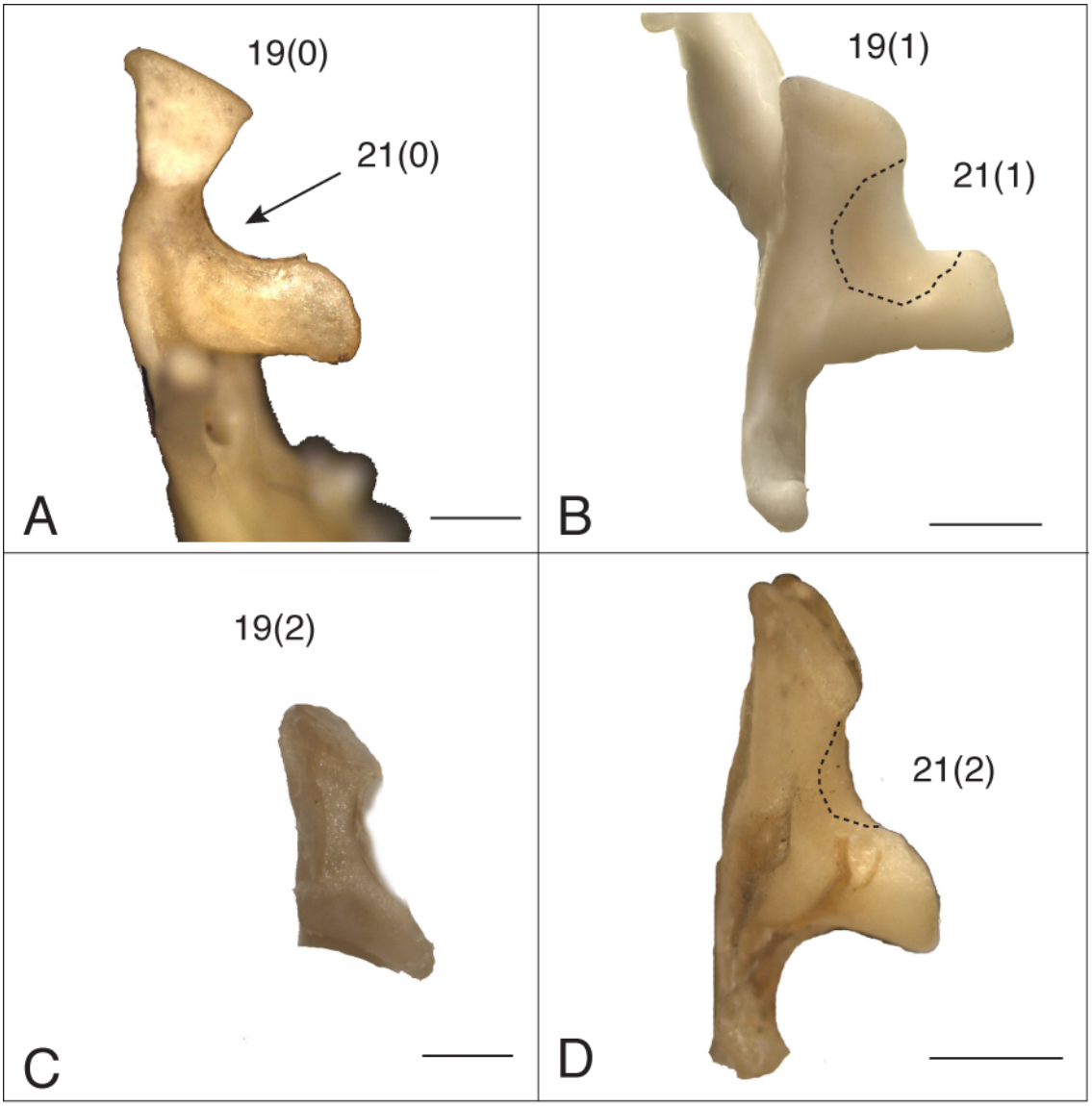


Figure 2.9: Character 19, Interarticular condyle area, and character 21, lingual side of interarticular area. Dashed lines indicate margin of interarticular basin. A. *Notiosorex crawfordi* (TTU 92929) B. *Blarina brevicauda* (TCWC 50101) C. *Sorex cinereus* (TCWC 26977) D. *Cryptotis goldmani* (TCWC 5575). See text for description of character states. Scale bar = 1mm.

This character was used by Repenning (1967) to differentiate Soricinae into three tribes. As defined by Repenning, Tribe Neomyini would have state 0, Tribe Blarinini state 1, and Tribe Soricini state 2. The condyles were figured by Carraway (1995, 2007) but were not given a character number.

The condyles of all *Crocidura* are different from Soricinae. There is a slight emargination on the labial side and not on the lingual side as found in Soricinae. I did not score *Crocidura russula* for this character. The state of *Megasorex gigas* and *Notiosorex crawfordi* was assigned state 0 (Fig. 2.9A). *Megasorex gigas* has a wide lower condyle, but the interarticular area was emarginated compared to the upper condyle. I did not assume an ancestral condition by assigning state 0 for this character state. In the most commonly accepted phylogeny of shrews, each state is equally parsimonious as the ancestral state. *Blarina* and *Cryptotis* both had state 1 (Fig. 2.9B), and *Sorex* had state 2 (Fig. 2.9C). These states were constant within each taxon.

Character 20: Articular condyle in labial view; 0 = short upper condyle and short overall length of condyle, 1 = short upper condyle and lower condyle distinct in lateral view, 2 = long upper condyle and lower condyle slight or absent from lateral view; Fig. 2.10 (Woodman and Timm, 1999, 2003, 7).

The character was described by Woodman and Timm (1999, 2003) as 'articular condyle; low and broad (0); high and narrow (1).' There was no description of the orientation of this character, or to what degree the condyle was low and broad, or high

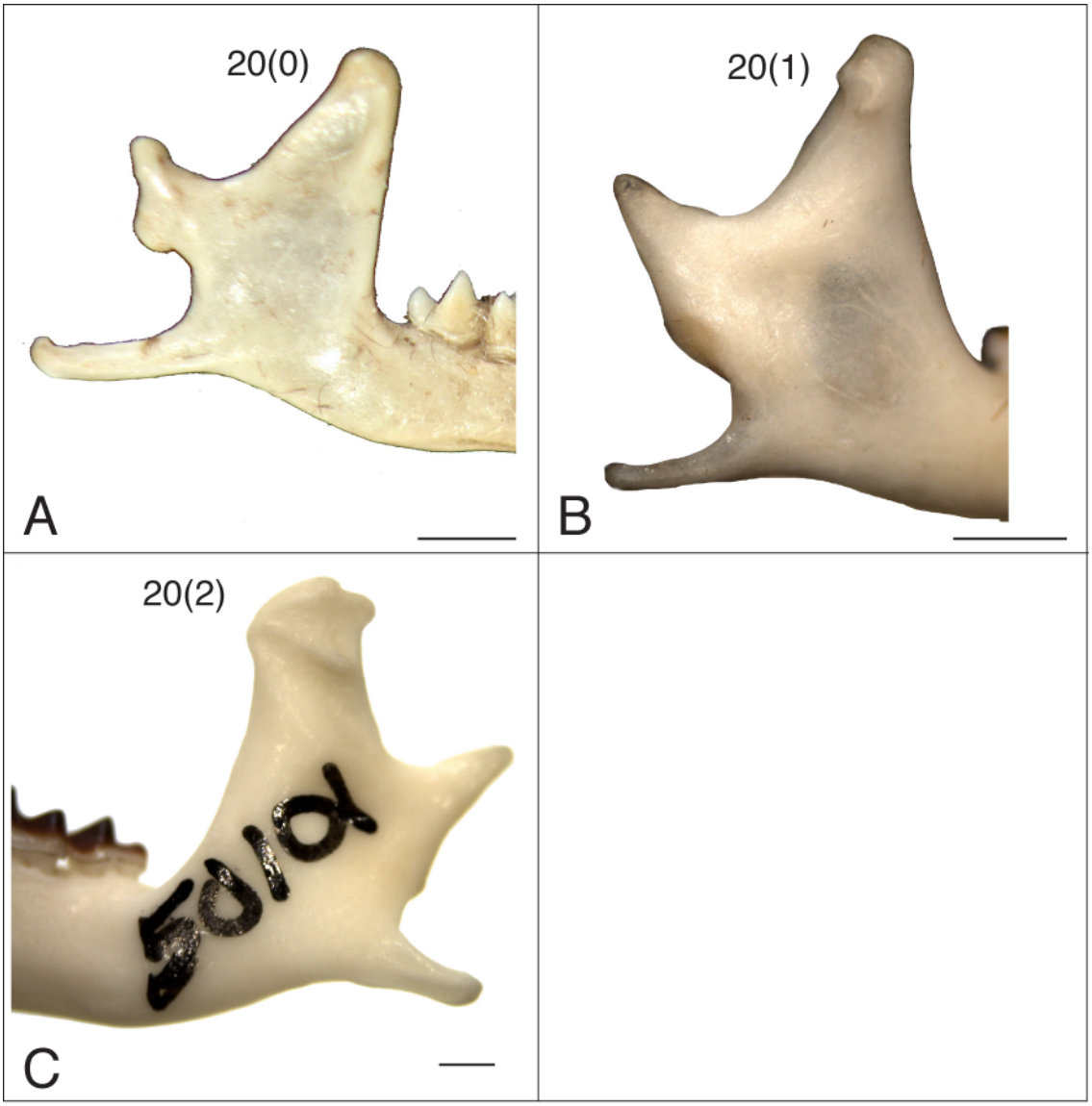


Figure 2.10: Character 20, articular condyle in labial view. A. *Crocidura russula* (TMM M-4130) B. *Cryptotis parva* (TCWC 50179) C. *Blarina brevicauda* (TCWC 50101). See text for description of character states. Scale bar = 1mm.

and narrow. I was unsure how to interpret these states, but there are distinct differences in the profile view of the labial side of the articular condyle. *Crocidura russula* shows a distinctly short upper condyle and short overall length of condyle relative to the length of the dentary. It is also short compared to other shrews; *Sorex arcticus*, *Sorex cinereus*, and *Sorex fumeus* had a similar short condyle. The upper condyle of *Megasorex gigas*, *Notiosorex crawfordi*, and *Cryptotis parva* were short, but the overall length of the upper and lower condyles together was much longer than in state 0. The lower condyle is also distinctly visible in lateral view. This contrasts with the lower condyle in *Blarina* and the other species of *Cryptotis*. It does not project from the rear of the dentary like in state 1. The upper condyle in state 2 is longer in lateral view than in either state 0 or 1.

Character 21: Lingual side of interarticular area; 0 = no basin, 1 = wide basin, 2 = slight basin; Fig. 2.9 (Carraway, 1995).

This was one of the characteristics used by Repenning (1967) to separate subfamilies of Soricidae. In Carraway (1995), *Blarina brevicauda* was separated from *Blarina carolinensis* and *Blarina hylophaga* by the presence of a basin in *Blarina brevicauda*. My observation was that all species of *Blarina* had an equally well-developed basin (Fig. 2.9B). I also observed a slight depression or basin in the interarticular area of *Cryptotis*, and I added state 2 to accommodate it (Fig. 2.9D). *Crocidura russula*, *Notiosorex crawfordi*, *Megasorex gigas,* and *Sorex* do not have any type of basin. *Crocidura russula* and *Sorex* have close-set condyles that do not have enough space for a

basin (Fig. 2.9C). *Notiosorex crawfordi* and *Megasorex gigas* have extremely emarginated interarticular areas that do not have a basin (Fig. 2.9A).

Character 22: Internal temporal fossa; 0 = large, 1 = medium, 2 = small; Fig. 2.11 (Rofes and Cuenca-Bescós, 2009, 41, 42).

The states used by Rofes and Cuenca-Bescós, (2009) for character 41 were 'internal temporal fossa: (0) large; (1) deep' and for character 42 'internal temporal fossa position: (0) low extended; (1) low.' I could not discern the intent of their character state description. A superior and inferior opening to the internal temporal fossa was described by Carraway (1995). The fossa was described as separated by a bar, a narrow raised segment that would divide the internal temporal fossa into superior or inferior regions. I observed a bar in some specimens, but in most the bar was so subtle that I could not use it reliably as a character.

I greatly simplified the scoring of this character because I could easily differentiate the size of the internal fossa into three categories. The large fossa (0) takes up most of the lingual side of the coronoid process and extends deep into the dentary (Fig. 2.11A). The medium fossa (1) is a large hole but does not extend as far anteriorly up the coronoid process as does the large fossa (Fig. 2.11B). The small fossa (2) is a fairly round hole in the lingual side of the dentary at the base of the coronoid process (Fig. 2.11C). This character varied greatly between specimens of *Blarina carolinensis, Blarina hylophaga, Cryptotis parva, Cryptotis mexicana*, *Cryptotis magna, Megasorex gigas, Notiosorex*

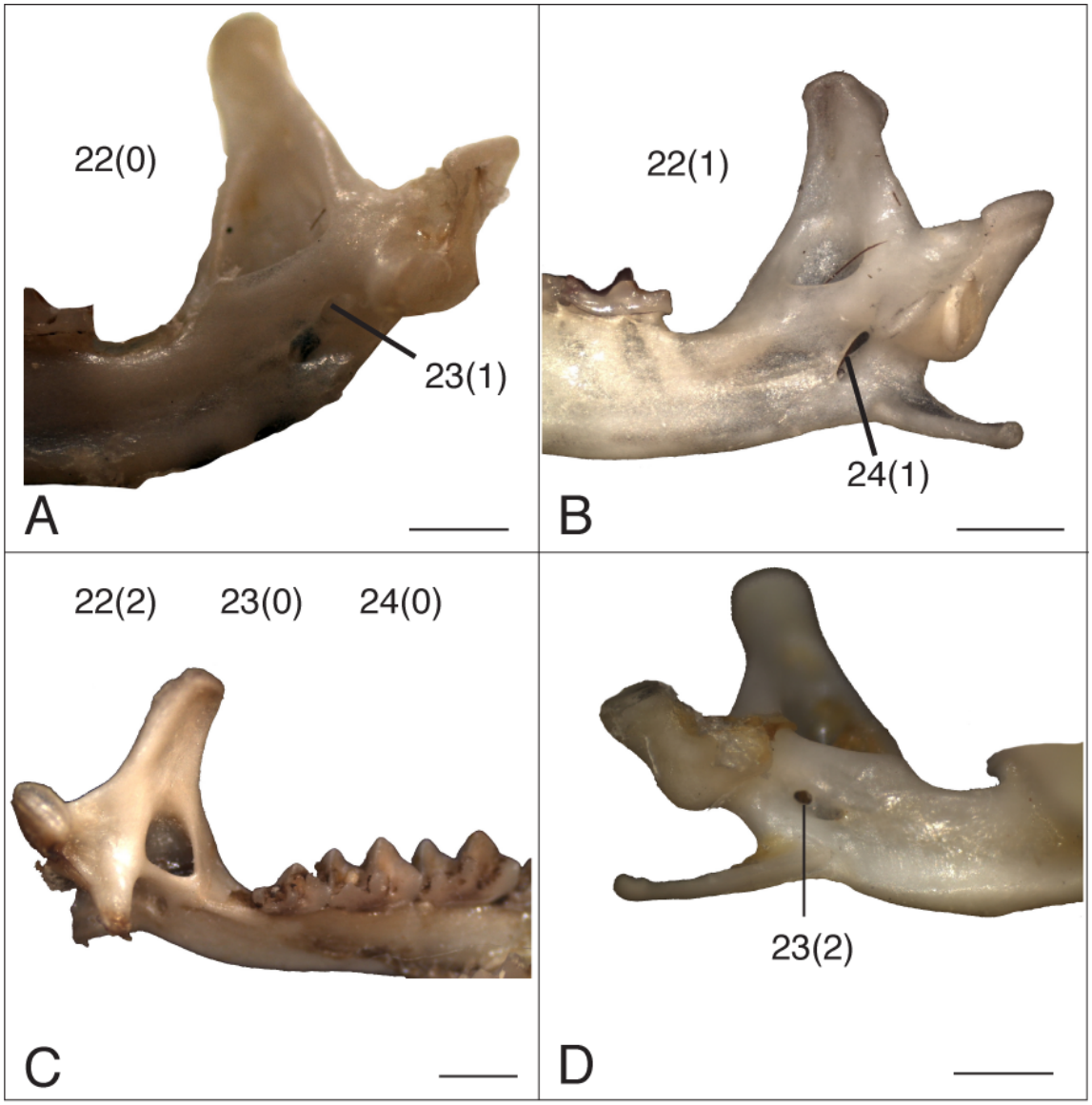


Figure 2.11: Character 22, Internal temporal fossa; character 23, canal into temporal fossa; character 24, mandibular canal. A. *Sorex trowbridgii* (TCWC 45855) B. *Cryptotis parva* (TCWC 50182) C. *Notiosorex crawfordi* (TCWC 31606) D. *Sorex fumeus* (TCWC 6564). See text for description of character states. Scale bar = 1mm.

crawfordi, and *Sorex vagrans*. *Blarina carolinensis* and *Blarina hylophaga* showed all three states, but *Blarina brevicauda* only had a large fossa.

Character 23: Canal into temporal fossa; 0 = absent, 1 = present, well-developed, 2 = tiny hole; Fig. 2.11 (Zaitsev and Rzebik-Kowalska, 2003).

This was referred to as the mandibular/postmandibular [sic] foramina complex (MPF-complex) by Zaitsev and Rzebik-Kowalska (2003). They described three morphotypes, but they are different from my states. Morphotype A corresponds to my state 0 and morphotype B to my state 1. They mention that other variations of this character exist including a small hole. I defined that small hole as my state 2. They only examined *Sorex* and that might explain the difference in the expression of this character. They found that in some taxa this was polymorphic. In their key to North American *Sorex,* Junge and Hoffman (1981) used the post-mandibular canal to differentiate the subgenus *Otisorex* from subgenus *Sorex*.

I found that this character was variable. There was a continuum between a well-developed canal (state 1, Fig. 2.11A) and the tiny hole (state 2, Fig. 2.11D). This is why the qualifier 'well-developed' was added to state 1. The variation of this character in *Sorex* was documented by Zaitsev and Rzebik-Kowalska (2003). I observed a great deal of variation, including different states between the left and right dentary of a few individuals. Individual variation among all taxa compromises the utility of this character for identification.

Character 24: Mandibular canal; 0 = separate from temporal fossa, 1 = close to/connecting to canal into temporal fossa; Fig. 2.11 (modified from Rofes and Cuenca-Bescós, 2009, 46).

This character was described as 'Mandibular foramen connected to the internal temporal fossa: (0) never; (1) frequently' by Rofes and Cuenca-Bescós (2009). It is difficult to differentiate whether the mandibular canal should be scored as separate from the temporal fossa or 'close' to the canal into the temporal fossa. This may be why the states listed by Rofes and Cuenca-Bescós (2009) are 'never' or 'frequently.' I scored this character as state 1 when the mandibular canal was immediately adjacent to the canal that passes into the temporal fossa, and found within a depression that surrounds both of them (Fig. 2.11B).

Individuals of *Blarina*, *Cryptotis*, and *Sorex trowbridgii* have a mandibular canal that connects to the canal into temporal fossa. However, *Blarina brevicauda* and all *Cryptotis* were polymorphic for this character, except *Cryptotis goldmani*.

Upper Dentition

Character 25: Pigment on I1; 0 = tip of I1 and posterior cusplet, 1 = all over; Fig. 2.12 (modified from Carraway, 1995).

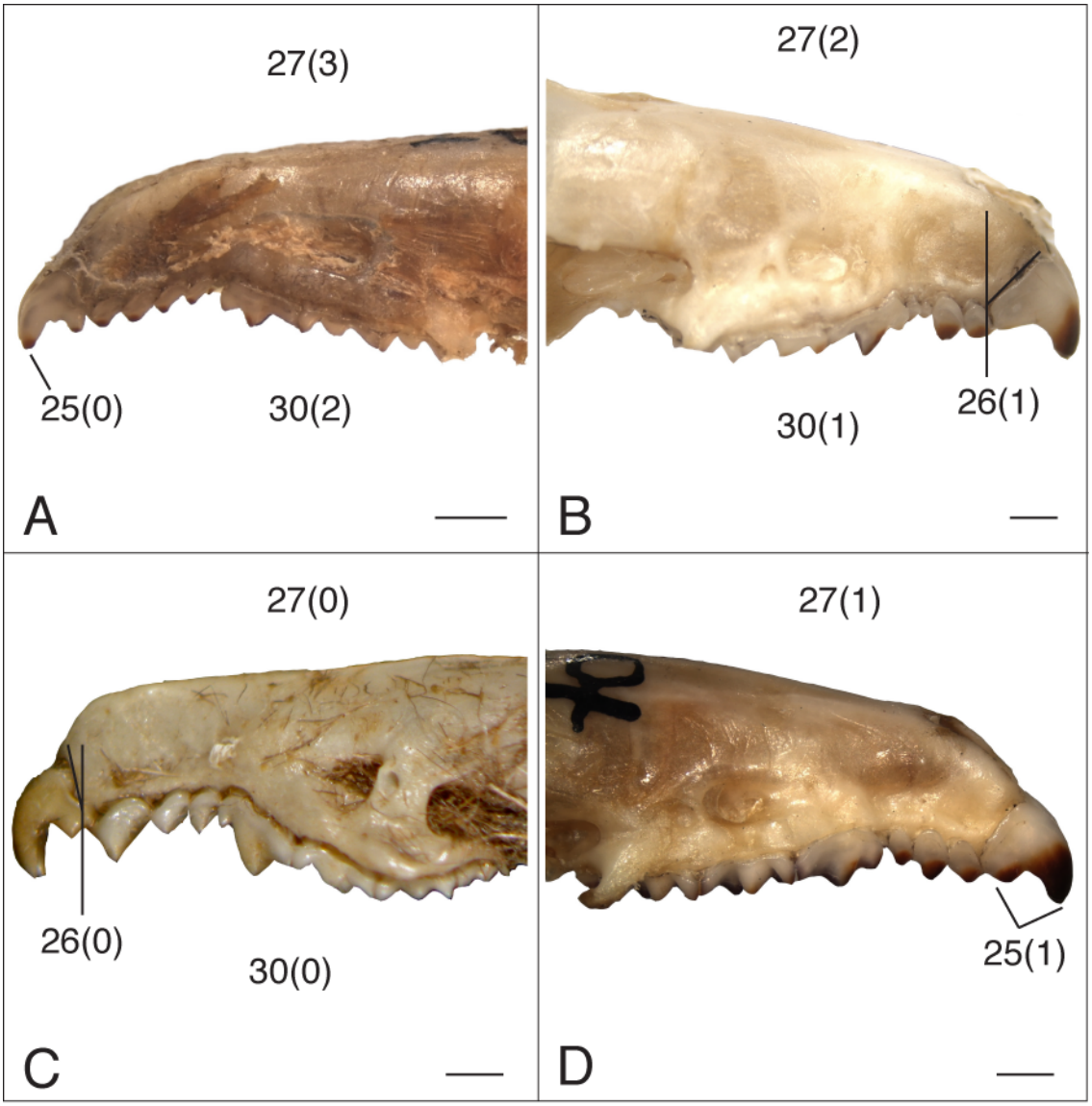


Figure 2.12: Character 25, pigment on I1; character 26, I1 alveolus orientation; character 27, number of upper antemolars; character 30, relative size of antemolars. A. *Sorex fumeus* (TCWC 20652) B. *Blarina hylophaga* (TCWC 31837) C. *Crocidura russula* (TMM M-4130) D. *Cryptotis goldmani* (TCWC 5665). See text for description of character states. Scale bar = 1mm.

This character is a description of how high up from the tip of the upper incisor the pigment extends. The pigment is either restricted to the tip of the incisor and sometimes the posterior cusplet (Fig. 2.12A) or covers most of the anterior of the tooth as well as extending to the posterior cusplet (Fig. 2.12D). This was used to separate species of *Sorex* by Carraway (1995). I found that it was variable within *Blarina brevicauda, Notiosorex crawfordi,* and *Sorex arcticus*. None of the *Crocidura* species or *Megasorex gigas* I examined had pigment on their teeth so this character was not scored for them. I chose not to score the absence of pigment as a character so as not to homologize the absence of pigment.

Character 26: I1 alveolus orientation in lateral view; 0 = vertical, 1 = angled down; Fig. 2.12.

I adapted this character from keys by Guilday (1962) and Carraway (1995). There seems to be some constancy to the orientation of I1 as it projects from the pre-maxilla. State 0 indicates that the I1 erupts straight out of the premaxilla in the anterior direction (Fig. 2.12C). State 1 differs from this by having a ventral component to the direction that the I1 erupts (Fig. 2.12B). However, this is difficult to quantify, so I only recognize two states. *Blarina brevicauda, Blarina carolinensis, Cryptotis magna, Notiosorex crawfordi,* and *Sorex fumeus* were polymorphic for this character.

Character 27: Number of antemolars per upper jaw; 0 = three, 1 = four, 2 = four visible in lateral view (five present), 3 = five visible in lateral view; Fig. 2.12 (modified from Woodman and Timm, 1999, 2003, 28; Carraway, 2007, 6, 7; Rofes and Cuenca-Bescós, 2009, 4).

The number of upper antemolars was used by many authors to separate genera of North American shrews (e. g., Repenning, 1967; Jones and Manning, 1992; Carraway, 1995). As a phylogenetic character, the number of antemolars was used in a variety of ways. The simplest had a number of states equal to the number of antemolars (Rofes and Cuenca-Bescós, 2009). Alternatively, this character was modified to a binary character where the only states were 'upper unicuspid toothrow: crowded, three unicuspids visible in lateral view (0); uncrowded, four unicuspids visible in lateral view (1)' (Woodman and Timm, 1999, 2003). Another form is to break it into two characters, '6. Number of unicuspids (= U)—3, 4, or 5; 7. Position of U4 in lateral view—completely visible, partially obscured, or not visible' (Carraway, 2007).

My observations corroborate what other authors found. All specimens I examined of *Crocidura*, *Megasorex gigas*, and *Notiosorex crawfordi* have three unicuspids (Fig. 2.12C) and *Sorex* spp. have five (Fig. 2.12A). The number of antemolars is more variable in *Cryptotis* spp. (Fig. 2.12D) and *Blarina* spp. (Fig. 2.12B). Dental abnormalities were reported previously for *Blarina* (Choate, 1968). I noticed several that lost U5 on one side or the other. The rate of subnumery teeth reported by Choate was around three

percent. I observed a rate near thirty percent. This difference probably results from the much smaller sample size I examined.

Character 28: Conical accessory cusp on upper antemolars; 0 = absent, 1 = present; Fig. 2.13 (Rofes and Cuenca-Bescós, 2009, 5).

My character is identical to that used by Rofes and Cuenca-Bescós (2009). Although the antemolars are often called unicuspids, this term is a misnomer because many upper antemolars have more than one cusp. Some antemolars have a simple, conical shape and are 'unicuspid' (Fig. 2.13B). Others are wide and have an extra cusp on the posterolingual side (Fig. 2.13A). Some specimens of *Cryptotis goldmani* and *Cryptotis parva* had accessory cusps and some did not. All other taxa I examined clearly have accessory cusps or do not.

Character 29: Broad upper antemolars; 0 = present, 1 = absent; Fig. 2.13 (Woodman and Timm, 1999, 2003, 9).

Antemolars were described as bulbous by Choate (1970), and were said to be characteristic of members of the *Cryptotis mexicana*-group. A variant of this character was used by Woodman and Timm (1999, 2003). Their character was 'shape of unicuspids (UI_V3): cone-shaped, posteroventral border straight-edged or convex (0); narrow, posteroventral border concave (1).'

I simplified this character because I could not reliably determine the difference between cone-shaped and narrow. Broad upper antemolars are larger and wider (Fig. 2.13A) than the simple conical antemolars found in most shrews (Fig. 2.13B). State 0

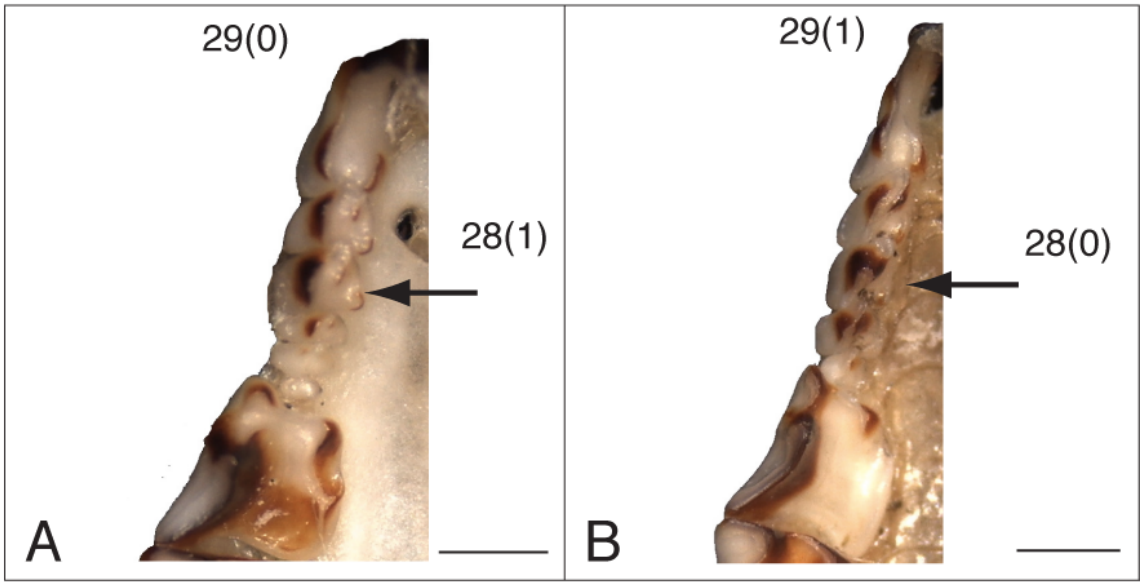


Figure 2.13: Character 28, conical cusp on antemolars, arrow indicates the accessory cusp (A) or the lack of an accessory cusp (B); character 29, broad antemolars. A. *Blarina carolinensis* (TCWC 33359) B. *Cryptotis goldmani* (TCWC 5665). See text for description of character states. Scale bar = 1mm.

does not require a secondary cusp on the antemolars, but taxa with secondary cusps also tend to have broad antemolars.

Character 30: Relative size of upper antemolars, 0 = 1st antemolar (A1) large, 1 = 2nd antemolar (A2) large (taller than A1), 2 = A1 and A2 equal in size; Fig. 2.12.

This is a new character. The difference in the relative size of A3 and A4 was used to separate species of *Sorex* by Junge and Hoffman (1981). There were two characters addressing the relative size of upper antemolars discussed by Carraway (2007). Her characters compared A3, A4, and A5. I did not notice a significant difference between A3 and A4. I observed A5 to be the smallest antemolar in all shrews, or equivalent in size to the smallest. A5 did not vary relative to A3 or A4.

State 0 was distinct when present (Fig. 2.12C). The A1 in *Crocidura russula* is approximately 50% larger than the other antemolars. In taxa where A2 is the largest antemolar, it is only slightly larger than A1, and can appear to be taller (from root to tip) than it is large (Fig. 2.12B). It is distinctly larger than A3. The antemolars of *Sorex* spp. are typically the most nearly equal in size (Fig. 2.12A).

Character 31: Protoconal basin of M1; 0 = smaller than hypoconal basin, 1 = equal to or larger than hypoconal basin; Fig. 2.14 (Woodman and Timm, 1999, 2003, 10).

This character was taken directly from Woodman and Timm (1999, 2003), however the states are reversed because I assigned state 0 to the condition found in *Crocidura russula*. This characteristic was also used in a key for North American shrews to separate *Cryptotis parva* from other *Cryptotis* (Hall, 1981). For most of the specimens I examined the hypoconal basin was equal to the protoconal basin or slightly larger (Fig. 2.14B). Only *Cryptotis magna* had state 0, and was not polymorphic (Fig. 2.14A). *Blarina brevicauda, Blarina hylophaga, Cryptotis goldmani*, *Cryptotis parva*, and *Notiosorex crawfordi* were polymorphic.

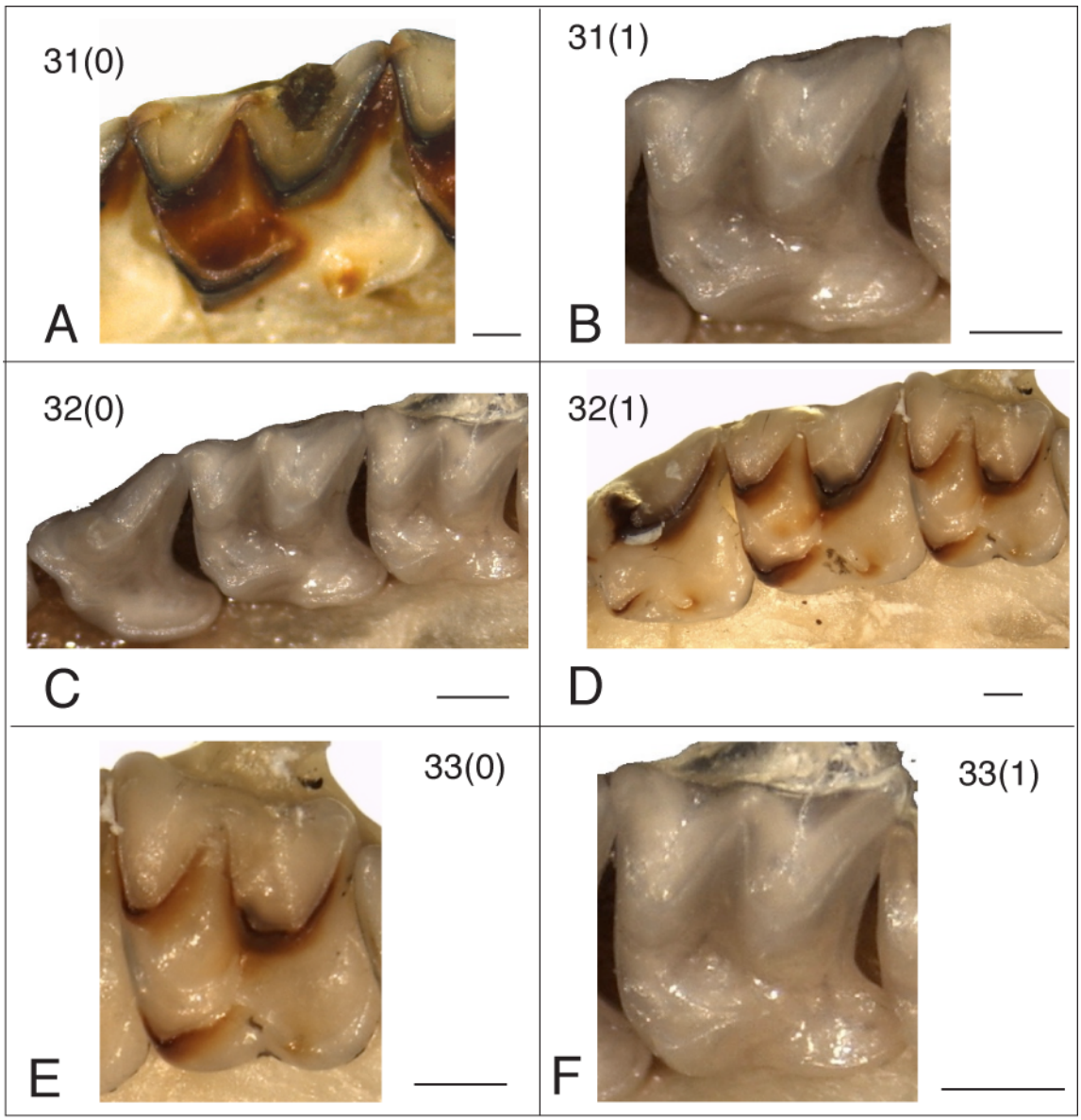


Figure 2.14: Character 31, protoconal basin of M1; A. *Cryptotis goldmani* (TCWC 5575) B. *Notiosorex crawfordi* (TTU 9728). Character 32, posterior border of P4, M1, and M2; C. *Notiosorex crawfordi* (TTU 9728) D. *Blarina hylophaga* (TCWC 31837). Character 33, Shape of M2; E. *Blarina hylophaga* (TCWC 31837) F. *Notiosorex crawfordi* (TTU 9728). See text for description of character states. Scale bar = 0.5 mm.

Character 32: Posterior border of P4, M1, and M2; 0 = strong emargination, 1 = slight to no emargination; Fig. 2.14.

This character was used by Hall (1981) in his key to North American mammals to separate *Notiosorex crawfordi* from *Megasorex gigas*. It can be used distinguish the two because *Notiosorex crawfordi* has extremely emarginated molars and the molars of *Megasorex gigas* are straighter posteriorly. However, I found one individual of *Megasorex gigas* with emarginate molars.

Most of the species of shrews I examined had strongly emarginated molars (Fig. 2.14C). Slight to no emargination was common within Blarinini (Fig. 2.14D). All *Blarina*, *Cryptotis mexicana,* and *Cryptotis magna* did not have emarginated molars. *Cryptotis goldmani* was polymorphic. *Cryptotis parva* was the only species in Blarinini to consistently have emarginated molars.

Character 33: Shape of the occlusal outline of M2; 0 = trapezoidal, 1 = rectangular; Fig. 2.14 (Rofes and Cuenca-Bescós, 2009, 12).

This character was used to distinguish *Blarina* from other Blarinini (sensu Repenning, 1967). All *Blarina* have a trapezoidal M2, but so do *Crocidura russula* and most species of *Cryptotis* (Fig. 2.14E). *Cryptotis parva* and *Cryptotis mexicana* were polymorphic, as were several species of *Sorex*. As I scored this character, it could not separate *Blarina* from other Blarinini.

I do not know how this character was interpreted by Rofes and Cuenca-Bescós (2009). Their state 0 was rectangular. I found that this agreed with my results, and all specimens of *Sorex* had a rectangular M2 (Fig. 2.14F).

Character 34: M3 cusp morphology; 0 = simplified, 1 = well developed; Fig. 2.15 (Woodman and Timm, 1999, 2003, 11).

I modified this character from Woodman and Timm, (1999, 2003). Their description addressed whether the metacone was absent or present. I noted a greater range of variation between M3s, probably because Woodman and Timm were only examining species within *Cryptotis*. Some taxa, like *Sorex,* have well developed M3s with multiple cusps that were as well developed as the cusps on M1 and M2 (Fig. 2.15B). The simplified cusps are lower and less distinct (Fig. 2.15A). The only other taxon with consistently well-developed M3 cusp morphology was *Megasorex gigas. Blarina brevicauda, Blarina hylophaga*, and *Cryptotis goldmani* were polymorphic.

Cranium

Character 35: Anterior extent of zygomatic process of maxilla; 0 = originates opposite mesostyle of M2, 1 = to posterior part of M2, 2 = absent; Fig. 2.15.

The origin of the zygomatic process of the maxilla relative to the dentition varies between taxa. When looking at the ventral surface of the skull, the zygomatic process will either project from the mesostyle (middle) of M2, or from a point posterior to the

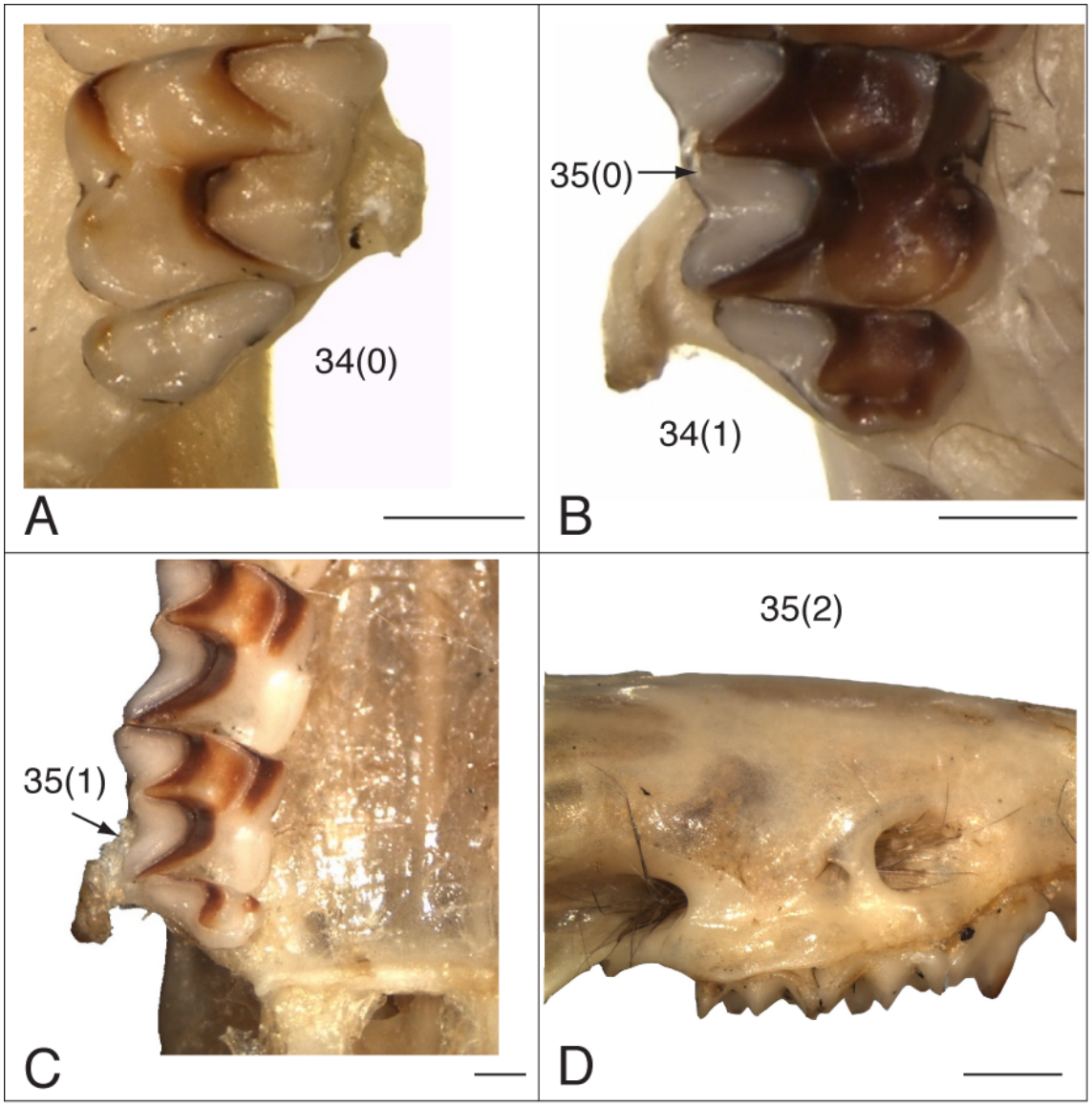


Figure 2.15: Character 34, M3 cusp morphology; character 35, anterior extent of zygomatic process of maxilla. A. *Blarina hylophaga* (TCWC 31837) B. *Blarina brevicauda* (TCWC 50105) C. *Cryptotis goldmani* (TCWC 5665) D. *Notiosorex crawfordi* (TTU 92929). See text for description of character states. Scale bar = 1 mm.

mesostyle of M2. *Blarina*, *Cryptotis parva,* and *Sorex bendirii* all show the primitive state for this character (Fig. 2.15B). The other species of *Cryptotis* and *Sorex* exhibited state 1 (Fig. 2.15A). *Notiosorex crawfordi* and *Megasorex gigas* do not have a zygomatic process and were scored as absent for this character (Fig. 2.15D).

Character 36: Posterior extent of zygomatic process in ventral view; 0 = not past M2, 1 = to middle of M3, 2 = to posterior edge of M3 or beyond, 3 = to anterior edge of M3; Fig. 2.16 (modified from Carraway, 2007)

This character was illustrated in two figures by Carraway (2007), but not formalized as a character. The figures in Carraway (2007) show my states 3 and 1. I observed greater variation in the length of the zygomatic process and created two additional states to accommodate the variation.

Notiosorex crawfordi and *Megasorex gigas* do not have a zygomatic process and were not scored for this character. All *Blarina* show state 3 and there is no individual variation (Fig. 2.16D). State 2 was present in all *Cryptotis* (Fig. 2.16C) except *Cryptotis parva*, which has state 1 (Fig. 2.16B). Those two states were reversed in *Sorex*, where all are state 1 except *Sorex bendirii*, which has state 2. All specimens of *Crocidura* I examined had state 0 (Fig. 2.16A).

Character 37: Shape of zygomatic process; 0 = short, 1 = absent, 2 = wide, 3 = long; Fig. 2.17 (Carraway, 2007, 11).

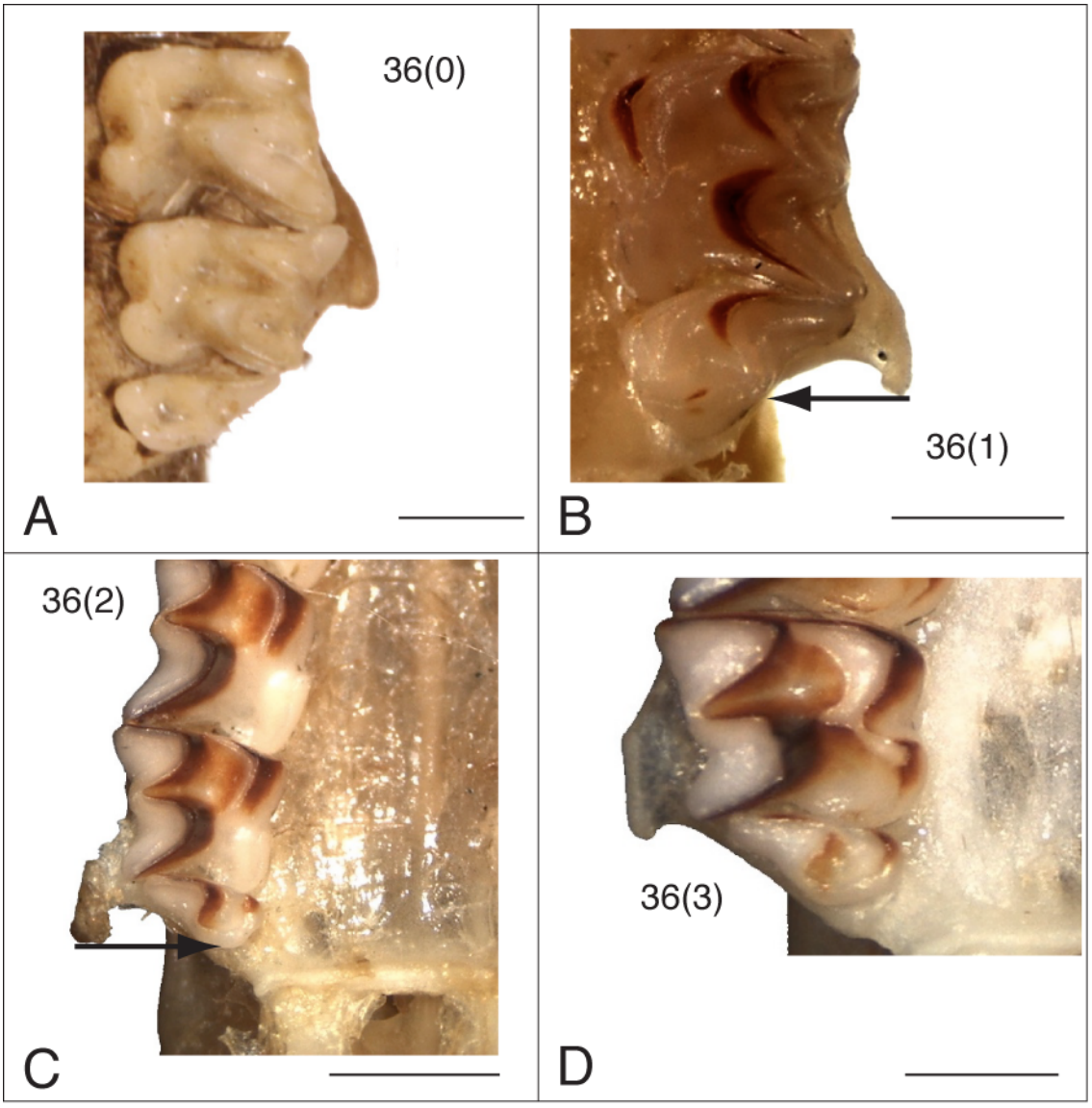


Figure 2.16: Character 36, Posterior extent of zygomatic process in ventral view. A. *Crocidura russula* (TMM M-4130) B. *Sorex trowbridgii* (TCWC 45855) C. *Cryptotis goldmani* (TCWC 5665) D. *Blarina carolinensis* (TCWC 33359). Arrows show farthest extent of zygomatic process. See text for description of character states. Scale bar = 1 mm.

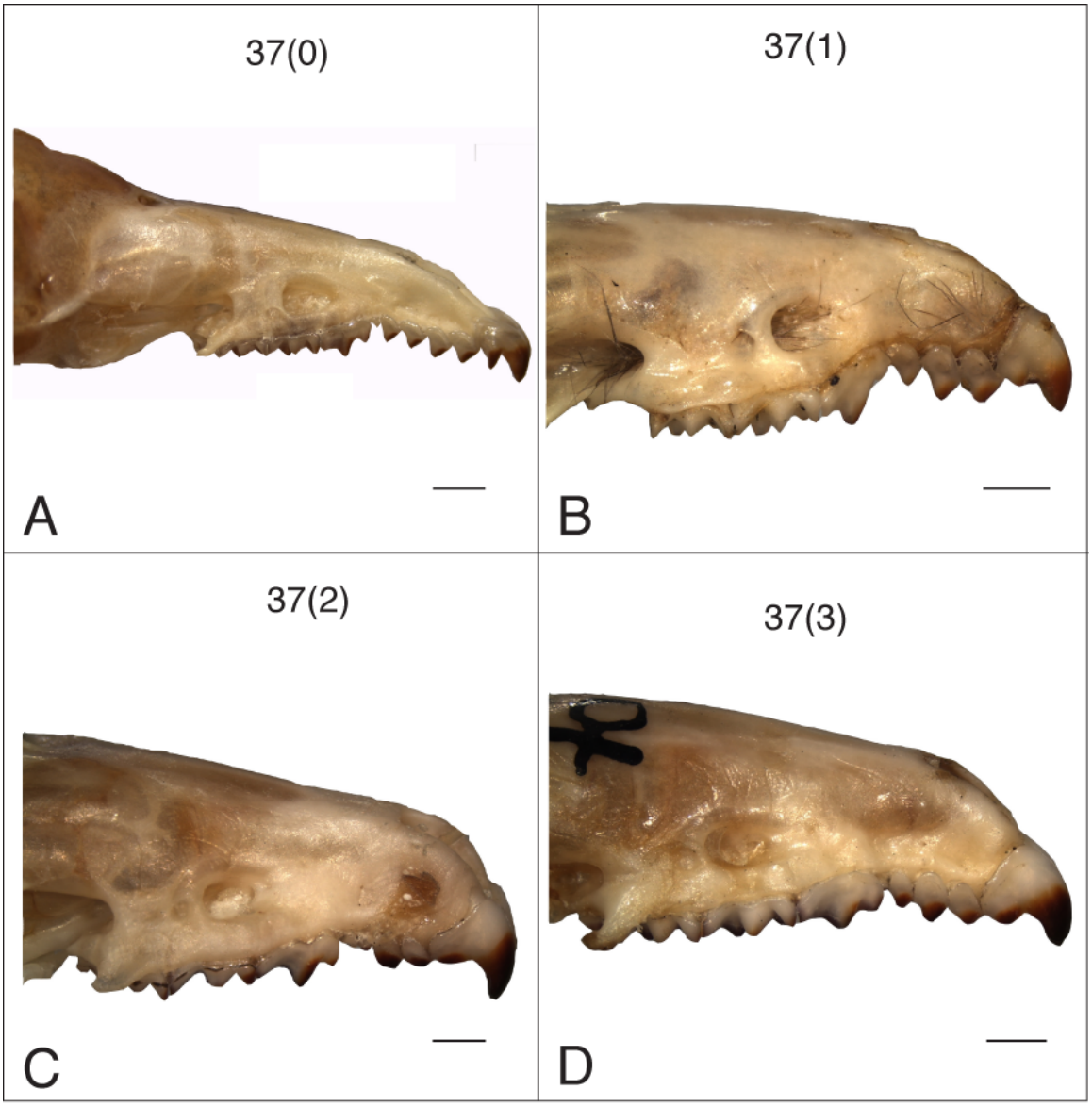


Figure 2.17: Character 37, Shape of zygomatic process. A. *Sorex cinereus* (TCWC 26799) B. *Notiosorex crawfordi* (TTU 92929) C. *Blarina carolinensis* (TCWC 33339) D. *Cryptotis goldmani* (TCWC 5665). See text for description of character states. Scale bar = 1 mm.

The zygomatic process was described as a character by Carraway (2007), having four states, which were sharply pointed, medium-large, bulbous, and elliptic. These complicated descriptions were figured, but I could not differentiate them in the specimens I examined. I simplified them to the four states listed above. Short zygomatic processes only project a millimeter or less posterolaterally from the lateral side of the skull (Fig. 2.17A). I found that state in *Crocidura russula, Blarina carolinensis, Cryptotis parva, Sorex cinereus, Sorex fumeus, Sorex trowbridgii,* and *Sorex vagrans*. The wide zygomatic process is about the same length as the short process, but it is at least twice as wide (Fig. 2.17C). That state was found in *Blarina brevicauda, Blarina hylophaga*, and *Cryptotis magna*. The long process projects about twice as far as the short process and is much more slender (Fig. 2.16D). That was found in *Cryptotis goldmani, Cryptotis mexicana, Sorex arcticus,* and *Sorex bendirii*. *Sorex cinereus* was polymorphic has both states 0 and 3.

Character 38: Zygomatic process extends ventrolateraly below occlusal surface in lateral view; 0 = absent, 1 = present; Fig. 2.18 (Carraway, 2007, 10).

This character was modified to simplify the original scoring of four states, 'flare laterally, project ventrally, extend posteriorly, or extend dorsoventrally' (Carraway, 2007). Though this character was also figured (Carraway, 2007: Figure 28-29, p. 12), I could not reliably score these states in the taxa I examined. I did observe that in some taxa the process would extend below the teeth when the skull is viewed from the lateral side. To

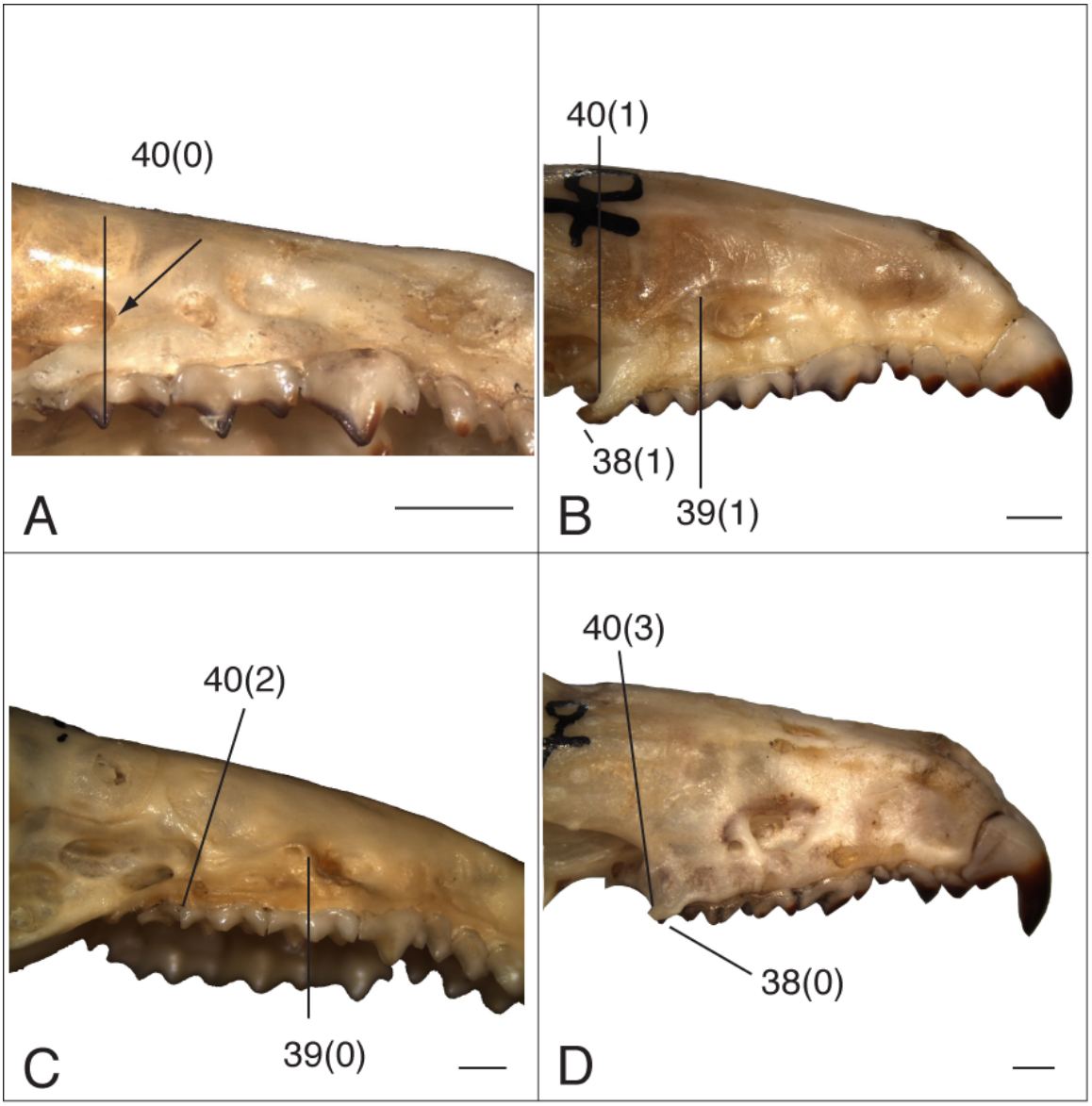


Figure 2.18: Character 38, zygomatic process extends below occlusal surface in lateral view; character 39, location of anterior end of zygomatic plate; character 40, location of posterior end of zygomatic plate. A. *Sorex vagrans* (TCWC 20650) B. *Cryptotis goldmani* (TCWC 5665) C. *Megasorex gigas* (TCWC 5828) D. *Blarina brevicauda* (TCWC 23684). See text for description of character states. Scale bar = 1 mm.

determine whether the process would extend below the molars, I held the skull so that I was observing the skull as precisely in lateral view as possible. This is scored as state 1 (Fig. 2.18B). I observed that state in *Cryptotis goldmani, Cryptotis mexicana, Cryptotis magna, Sorex arcticus,* and *Sorex bendirii*. *Cryptotis magna* and *Sorex arcticus* were polymorphic. All taxa that I scored as long (character 37:3) also have zygomatic processes that extend below the occlusal surface of the teeth, but *Cryptotis magna* was scored as wide (character 37:2), and some specimens of that taxon have zygomatic processes that extend below the occlusal surface of the teeth.

Character 39: Location of anterior end of zygomatic plate; 0 = in line with the mesostyle of M1, 1 = in between M1 and M2; Fig. 2.18 (modified from Choate, 1970).

Shrews lack zygomatic arches, but the homologous area of the maxilla was described as the zygomatic plate by Choate (1970). He argued that through the evolutionary history of *Cryptotis* the zygomatic plate shifted to a posterior position. Though he did not discuss this from a phylogenetic perspective, my results support Choate's interpretation. Based on the phylogenies of Brant and Ortí (2002), Grenyer and Purvis (2003), and Ohdachi et al. (2006), the more derived species, *Cryptotis goldmani*, *Cryptotis mexicana,* and *Cryptotis magna* have the zygomatic plate in a more posterior position (Fig. 2.18B) compared to the other shrews I examined (Fig. 2.18C).

Character 40: Location of posterior end of zygomatic plate; 0 = anterior to mesostyle of M2, 1 = even with or anterior to the anterior extent of the zygomatic process, 2 = posterior to M2, 3 = posterior to M2 and confluent with posterior base of the zygomatic process; Fig. 2.18 (modified from Choate, 1970; Woodman and Timm, 1999, 2003, 5).

This character was illustrated by Choate (1970) and Woodman and Timm (1999, 2003), but I substantially modified it from their descriptions. The posterior edge of the zygomatic plate is commonly emarginated anteriorly. The states of this character attempt to describe the variation in degree of emargination. The most emarginated condition is state 0 and is found in *Crocidura russula*, and all *Sorex* except *Sorex trowbridgii* (Fig. 2.18A). *Sorex fumeus* was polymorphic for state 0 and 2. State 1 is the next most emarginated and is as far anterior as the origin of the zygomatic process (Fig. 2.18B). That state is found in *Blarina carolinensis, Cryptotis parva*, and *Sorex trowbridgii*. *Notiosorex crawfordi* and *Megasorex gigas* have a distinct anterior margin, and lack zygomatic processes, so the posterior extent of the zygomatic plate is posterior to the M2 (Fig. 2.18C). State 3 describes the location of the posterior edge of the zygomatic plate with little to no emargination (Fig. 2.18D). That condition is found in *Blarina brevicauda, Blarina hylophaga, Cryptotis mexicana, Cryptotis goldmani*, and *Cryptotis magna*. It is also posterior to the M2, but more posterior than state 2.

Results of Phylogenetic Analysis

When all taxa were included in the PAUP analysis, I recovered two most parsimonious trees shown as a strict consensus tree in Figure 2.19A. All 40 characters were parsimony-informative, and there was no difference between ordered and unordered characters. Notiosoricini and Blarinini were both monophyletic, but *Sorex* and *Cryptotis* were paraphyletic. *Blarina* was the only multi-species genus found to be monophyletic.

I then ran an analysis excluding *Sorex bendirii*, *Sorex vagrans*, and *Sorex trowbridgii*. In that analysis, all genera and tribes were monophyletic (Figure 2.19B). That analysis more closely matched the other phylogenetic hypotheses of shrews (Grenyer and Purvis, 2003; Ohdachi et al., 2006). Some authors considered *Sorex* the most primitive Soricinae because of affinities with some fossil shrews (Repenning, 1967; Rofes and Cuenca-Bescós, 2009). However, in my results *Sorex* is sister to the Blarinini. This places it well within Soricinae and is congruent with the results of molecular phylogenies (Grenyer and Purvis, 2003; Ohdachi et al., 2006).

Though the generic relationships within Soricinae are resolved, the species-level relationships of the more speciose genera are unresolved. All recent analyses that included *Sorex* yielded unresolved trees and are not directly comparable to my results, or to any other phylogeny (Fumagalli et al., 1999; Grenyer and Purvis, 2003; Ohdachi et al., 2006). This is because no analyses have examined the same taxa. There is so little resolution in phylogenies of *Sorex* that comparisons between my results and the results of other authors are not possible. As I found when I eliminated some *Sorex* species from my analysis, taxon selection can have a profound impact on the phylogeny of shrews.

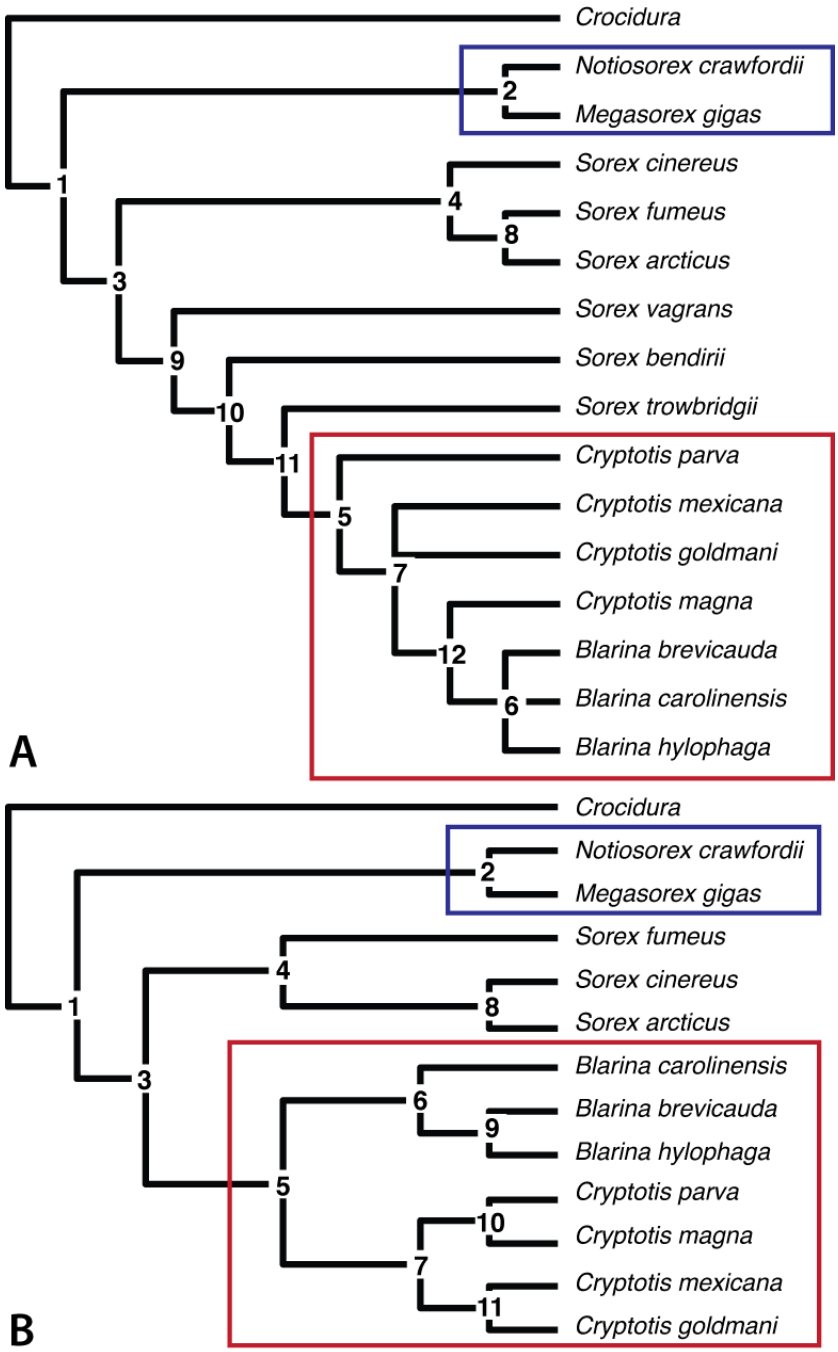


Figure 2.19: A: Strict consensus tree of the two most parsimonious trees generated by PAUP including all taxa examined in this study. B: The single most parsimonious tree generated by PAUP, excluding *Sorex vagrans, Sorex bendirii,* and *Sorex trowbridgii*. Red boxes indicate Blarinini and blue boxes indicate Notiosoricini.

Similar to the unresolved relationships of *Sorex*, there are no published phylogenies of the intrageneric relationships of *Notiosorex* or *Cryptotis* that include all named species. No one has published a phylogeny of *Notiosorex* since additional species were named (Carraway and Timm, 2000; Baker, O'Neill, and McAliley, 2003, Carraway, 2010). The existing phylogenetic hypotheses of *Cryptotis* include different taxa; therefore, the results vary between all published accounts (Grenyer and Purvis, 2003; Woodman and Timm, 2003; Ohdachi et al., 2006). Where there is resolution within *Cryptotis*, authors typically find *Cryptotis mexicana* and *Cryptotis goldmani* as sister taxa (Woodman and Timm, 1999, 2003; Grenyer and Purvis, 2003; Ohdachi et al., 2006). The strict consensus of my analysis of all taxa resulted in a paraphyletic *Cryptotis* with a polytomy between *Cryptotis mexicana, Cryptotis goldmani* and *Cryptotis magna* + *Blarina*. However, I recovered *Cryptotis mexicana* and *Cryptotis goldmani* as sister taxa in the pruned PAUP analysis (Fig. 2.19B)

The relationship of the species of *Blarina* is better resolved. Multiple authors previously recovered the relationships within *Blarina* to be *Blarina brevicauda* + *Blarina carolinensis* sister to *Blarina hylophaga* (Brant and Ortí, 2002 and Grenyer and Purvis, 2003). The phylogeny I generated with all taxa resulted in a polytomy for *Blarina* (Fig. 2.19A). In the pruned PAUP analysis *Blarina hylophaga* and *Blarina brevicauda* are sister taxa (Fig. 2.19B). In order to compare my results to prior workers, I traced my characters on a fully resolved tree that I arranged to be as consistent as possible with published phylogenetic hypotheses (Figure 2.20).

It is clear that a great deal of work still needs to be done before the relationships of Soricinae are fully resolved. However, I was most interested in characters that would be useful for identifying *Notiosorex crawfordi, Blarina*, and *Cryptotis* because these are shrews that are commonly found in Texas caves. The species of *Notiosorex* are difficult to

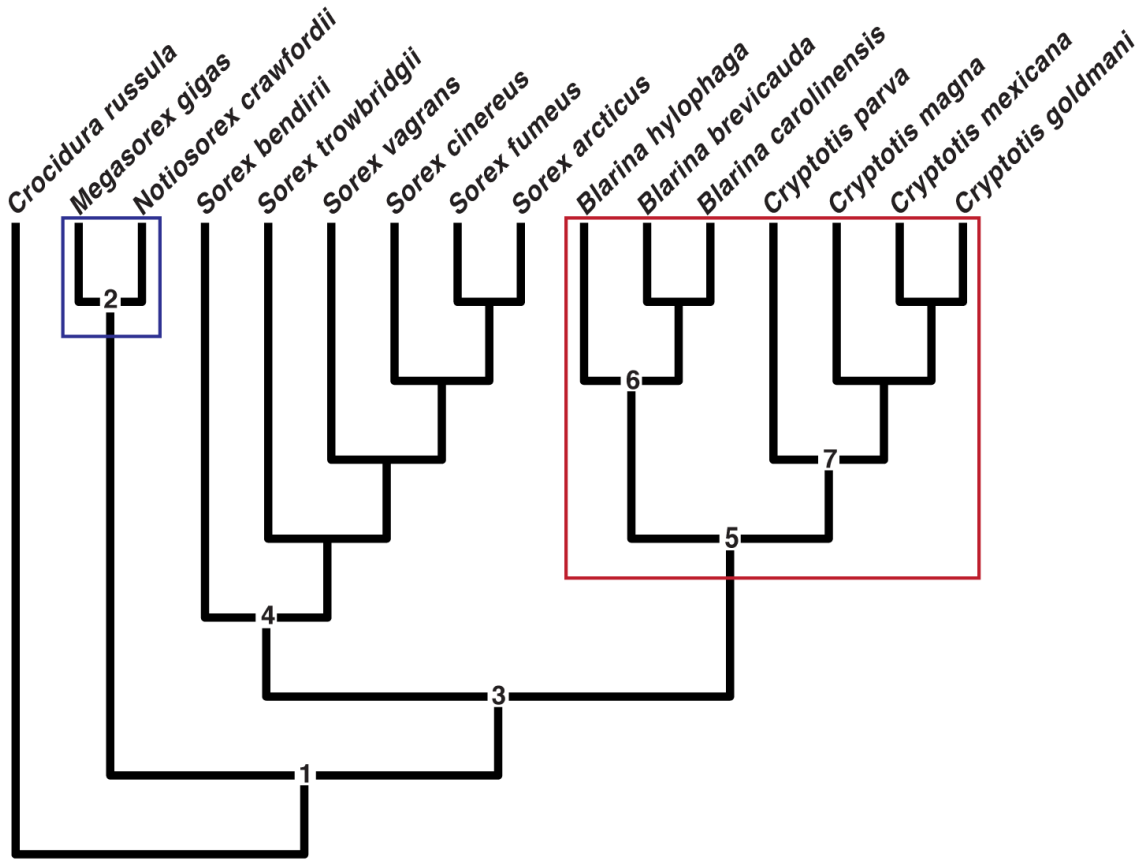


Figure 2.20: A composite phylogenetic hypothesis based on several molecular phylogenies (Brant and Ortí, 2002; Grenyer and Purvis, 2003; Ohdachi et al., 2006). Red box indicates Blarinini and blue box indicates Notiosoricini.

distinguish using morphology, and two species are restricted to small isolated populations in Mexico (Carraway and Timm, 2000; Baker, O'Neill, and McAliley, 2003). It will require a more detailed examination of the individual species of *Notiosorex* to determine which characters, if any can be used to reliably identify the species using apomorphies.

Discussion

Problematic characters

Several characters commonly used in keys and morphologic descriptions are problematic when used in broader phylogenetic contexts. These problems fell into several categories. One category includes characters that exhibited a large amount of intraspecific variation. I observed such a large degree of individual variation in the location of the mental foramen that I could not score it reliably for any taxon. However, it was reported previously that this character is fixed in some species of *Sorex* (Zaitsev and Rzebik-Kowalska, 2003). Of the 21 extant species examined by Zaitsev and Rzebik-Kowalska (2003), three exhibited a high degree of variation. I did not examine any of the species they used in their study.

Cingula of individual teeth or groups of teeth were used in previous morphological description (Graham and Semken, 1976) as well as phylogenetic analysis (Rofes and Cuenca-Bescós, 2009). Cingula of molars and pre-molars varied, as much between individuals as between taxa, so they were difficult to score. I have little confidence in the phylogenetic utility of those cingula. The presence or absence of the cingulum of i1 did not vary in 10 of 16 taxa; so I retained it as a character. The phylogenetic utility of this character is questionable.

Any of the characters that were subject to wear such as characters 2, 3, 7, 8, 10, 12, 25, 28, or 34, could be incorrectly scored if the individual tooth was worn to such a degree that the morphology of the tooth was changed (this was especially true of characters on i1). Most shrews live less than 18 months, but this is long enough for them to wear down their teeth. In extreme cases, wear could be so great that cusps could merge. Any individual I examined with that much wear was not scored for my analysis. However,

lightly worn specimens were scored exactly as they appeared, and this may have contributed to a small amount of the observed polymorphism.

Character transformations and synapomorphies

The synapomorphies listed in tables (2.3 to 2.10) and the primary discussion of those characters as synapomorphies are based on three trees: the two trees generated by PAUP (Fig. 2.19) and a composite molecular tree (Fig. 2.20). I traced characters using MacClade 4.08 (Maddison and Maddison, 2005). In cases where character state reconstructions were equivocal, I chose the most parsimonious reconstruction. This can yield different synapomorphies than assuming accelerated or delayed transformations; however, it is a more conservative estimate of which characters are synapomorphies.

The tables in this section list the characters that are potential synapomorphies for the clade followed by the change in state at that node. Nodes are labeled in Figs. 2.19 and 2.20, and congruent clades have the same numbers.

Node 1, Soricinae

I found several potential synapomorphies for Soricinae (Table 2.3). However, outside of Soricinae, I only examined *Crocidura*, and I suggest that these synapomorphies be considered tentative. These synapomorphies provide a basis for a larger examination of morphological evolution in all of Soricidae.

State 1 of character 9 is present in all ingroup taxa except *Cryptotis parva* and it is polymorphic in *Blarina carolinensis* and *Blarina hylophaga*. Character 30:2 is also a strongly supported synapomorphy. Character 10:1 is a potential synapomorphy for this

clade except that state 0 is found in *Sorex bendirii* and its position in the composite tree makes the transformation ambiguous at this node.

Table 2.3: Possible synapomorphies of Node 1, Soricinae.

PAUP (All Taxa)	**PAUP** (Pruned)	**Composite**
	5: 0 → 1	
9: 0 → 1	9: 0 → 1	9: 0 → 1
10: 0 → 1	10: 0 → 1	
30: 0 → 2	30: 0 → 2	30: 0 → 2
31: 0 → 1	31: 0 → 1	31: 0 → 1

Node 2, Notiosoricini

There are a large number of synapomorphies for this clade (Table 2.4). Characters 15, 17, 18, 20, 22, 33, 35, 37, and 40 are strongly supported synapomorphies and are found in all of the trees I examined.

In the composite tree, character 10 is a synapomorphy at this node as well as within *Sorex* and *Cryptotis*, instead of being a synapomorphy for node 1. Character 14 is likely a synapomorphy in the full PAUP tree, but *Notiosorex crawfordi* was polymorphic for this character so the character state reconstruction is ambiguous. This is also the case for character 26 in all trees. For characters 19, 20, 33, and 35, the ancestral state is equivocal, so I have listed the most likely state with a question mark.

Table 2.4: Synapomorphies of Node 2, Notiosoricini. * indicates ambiguity, ? indicates most likely state.

PAUP (All Taxa)	**PAUP** (Pruned)	**Composite**
		10: 0 → 1
14: 0 → 1*		
15: 0 → 1	15: 0 → 1	15: 0 → 1
17: 0 → 2	17: 0 → 2	17: 0 → 2
18: 0 → 1	18: 0 → 1	18: 0 → 1
19: 2? → 0	19: 2? → 0	19: 2? → 0
20: 0 → 1	20: 0 → 1	20: 0? → 1
22: 0 → 1/2	22: 0 → 1/2	22: 0 → 1/2
26: 0 → 1*	26: 0 → 1*	26: 0 → 1*
33: 0? → 1	33: 0 → 1	33: 0 → 1
35: 1? →2	35: 1? →2	35: 0 →2
37: 0 → 1	37: 0 → 1	37: 0 → 1
40: 0 → 2	40: 0 → 2	40: 0 → 2

Node 3

Although the topology of the PAUP tree differs significantly from the other two trees, there were still a number of common synapomorphies between all trees (Table 2.5). The unambiguous apomorphies are 3, 8, 11, and 16. Character 2 varies between state 2 and 3 within *Sorex*. Character 2:2 should be a synapomorphy for node 3, but in the full PAUP tree state 3 is ancestral and 2 is derived. Character 1 is only a synapomorphy in the PAUP tree with all taxa. That character is highly polymorphic so the reconstruction of the change in state at this node is equivocal in the other trees. Character 23 is also highly polymorphic and only a synapomorphy for this node in the pruned PAUP tree. In all trees a change from state 0 in character 19 and 27 happens at this node, but in the pruned PAUP tree and the composite tree the change to state 1 or 2 (or 3 for 27) is equally parsimonious. Character 20 is not a synapomorphy at this node for either PAUP tree

because *Sorex cinereus*, *Sorex fumeus*, and *Sorex arcticus* have state 0, or the plesiomorphic state.

Table 2.5: Synapomorphies at Node 3, * indicates ambiguity, ? indicates uncertain state.

PAUP (All Taxa)	**PAUP** (Pruned)	**Composite**
1: 0 → 2		
2: 0 → 3	2: 0 → 2	2: 0 → 2
3: 0 → 2	3: 0 → 1?	3: 0 → 1
8: 0 → 1	8: 0 → 1	8: 0 → 1
11: 0 → 1	11: 0 → 1	11: 0 → 1
16: 0 → 1	16: 0 → 1	16: 0 → 1*
19: 0? → 2		
		20: 0/1 → 2
	23: 0 → 2	
27: 0 → 3		
35: 2? → 1		
36: 0? → 1	36: 0? → 2	

Node 5, Blarinini

This clade is strongly supported by a number of synapomorphies (Table 2.6). The unambiguous synapomorphies common to all trees are 13, 18, and 19. Character 6 was ambiguous because it is polymorphic in several taxa and the ancestral state could not be reconstructed. Characters 5, 15, 21, 27, and 34 were only synapomorphies because of the different topology of the full PAUP tree. This difference in topology also led to characters 24, 32, and 40 being synapomorphies in the other two trees.

Table 2.6: Synapomorphies of Node 5, Blarinini, * indicates ambiguity.

PAUP (All Taxa)	**PAUP** (Pruned)	**Composite**
5: 0 → 2		
	6: 0 → 1*	6: 0 → 1*
13: 0 → 1	13: 0 → 1	13: 0 → 1
15: 0 → 2		
18: 0 → 1	18: 0 → 1	18: 0 → 1
19: 2 → 1	19: 2 → 1	19: 2 → 1
	20: 0 → 2	
21: 0 → 2		
	24: 0 → 1	24: 0 → 1
27: 3 → 1		
	32: 0 → 1	32: 0 → 1*
34: 1 → 0		
	40: 0 → 3	40: 0 → 3

Generic-level Clades

Node 4, Sorex

I did not examine the full diversity of *Sorex* so these potential synapomorphies are tentative (Table 2.7). When all examined taxa were included in the phylogenetic analysis, *Sorex* was paraphyletic (Fig. 2.19A). The only unambiguous apomorphy in the pruned PAUP tree and the composite tree was character 34. In the pruned PAUP tree, characters 1, 3, 14, 18, 19, 27, and 35 were ambiguous because the ancestral state could not be reconstructed. Characters 3 and 35 were only synapomorphies in the pruned PAUP tree and may just represent synapomorphies of this clade (node 4, Fig. 2.19B) within *Sorex* and not synapomorphies for *Sorex* as a whole.

Table 2.7: Possible synapomorphies of Node 4, *Sorex*, * indicates ambiguity, ? indicates most likely state.

PAUP (Pruned)	**Composite**
1: ? → 2	1: ? → 2*
3: ? → 2	
14: 1 → 0*	14: 1 → 0*
18: 1 → 0*	18: 1 → 0*
19: 0? → 2	19: 0? → 2
27: ? → 3	27: ? → 3
34: 0 → 1	34: 0 → 1
35: 0 → 1*	

Node 6, Blarina

Blarina was a monophyletic group in all the trees I examined. A large number of characters support the genus (Table 2.8). Characters 5, 21, 27, 28, 30, and 36 are strongly supported synapomorphies found in all trees. Character 15 is a plesiomorphy in the pruned PAUP tree and the composite tree. Character 17 is shared with *Cryptotis magna* and so is not a synapomorphy in the full PAUP tree.

None of my characters supported the sister taxon relationship of *Blarina carolinensis* and *Blarina brevicauda* that was recovered by other authors (Brant and Ortí, 2002; Reilly et al., 2005). The pruned PAUP tree resolved *Blarina hylophaga* and *Blarina brevicauda* as sister taxa. The characters that support this are 14, which is ambiguous because *Blarina carolinensis* is polymorphic for that character, and state 2 of character 37, which is found only in *Blarina hylophaga, Blarina brevicauda,* and *Cryptotis magna*. I am not suggesting that my results should overturn the established hypothesis of the relationships within *Blarina*, but there are potential problems differentiating members of *Blarina* using morphology. A single characteristic (angle of i1 >18 or <17 degrees to the

horizontal ramus of the dentary) separated *Blarina carolinensis* from *Blarina hylophaga* in Carraway's key (1995). I could not reliably measure that difference. The relationships of *Blarina* also are unresolved by molecular data. In one molecular phylogeny the genus *Blarinella*, an Asian shrew, was recovered within *Blarina* (Ohdachi et al., 2006). However, this is the only genus of North American shrews with a complete phylogeny. Using the characters in this study, it is possible to identify the species of *Blarina* with apomorphies.

Table 2.8 Synapomorphies of Node 6, *Blarina,* * indicates ambiguity, ? indicates unknown state.

PAUP (All Taxa)	**PAUP** (Pruned)	**Composite**
1: ? → 1	1: ? → 1	
5: 2 → 3	5: 1 → 3	5: ? → 3
10: 1 → 0	10: 1 → 0	
15: 2 → 0		
	17: 0 → 1	17: 0 → 1
21: 2 → 1	21: ? → 1	21: ? → 1
27: 1 → 2	27: ? → 2	27: ? → 2
28: 0 → 1*	28: 0 → 1*	28: 0 → 1*
30: 2 → 1	30: 2 → 1	30: 2 → 1
35: 1 → 0	35: 1 → 0*	
36: 2 → 3	36: 2 → 3	36: ? → 3

Node 7, Cryptotis

No one has yet published a complete phylogeny of *Cryptotis*, and I only examined a subset of species. Like *Sorex*, *Cryptotis* was paraphyletic in the full PAUP analysis. However, in the pruned PAUP tree and the composite tree *Cryptotis* is supported by a number of characters (Table 2.9). Characters 6, 7, 15, 21, and 27 strongly support this clade. The ancestral state is ambiguous for 5, 6, 21, 27, and 29. In the full PAUP analysis,

state 2 of characters 5, 15, 21, and state 1 of character 27 are synapomorphies for node 5, which includes *Cryptotis* and *Blarina*, but they change state for *Blarina*.

Cryptotis mexicana and *Cryptotis goldmani* are two members of the '*mexicana*' group. The full PAUP analysis resulted in a polytomy within *Cryptotis* but the pruned tree has *Cryptotis mexicana* and *Cryptotis goldmani* as sister taxa. Characters 37 and 38 are synapomorphies for this group in both the pruned PAUP tree and the composite. In the composite phylogeny, *Cryptotis mexicana* and *Cryptotis goldmani* have state 0 for characters 12 and 16 instead of state 1. These could be potential synapomorphies as well, but are interpreted as plesiomorphies in the pruned PAUP tree.

Table 2.9: Synapomorphies of Node 7, *Cryptotis,* * indicates ambiguity, ? indicates unknown state.

PAUP (Pruned)	**Composite**
	5: ? → 2*
6: 0 → 1*	6: 0 → 1*
7: 0 → 1	7: 0 → 1*
15: 0 → 2	15: 0 → 2
21: ? → 2	21: ? → 2
27: ? → 1	27: ? → 1
29: 0 → 1*	

Autapomorphies

My goals were to look at some of the variation within *Sorex* in order to at least make generic level identifications using apomorphies. The number of species of Sorex exceeds the characters in this study. My goal was not to find apomorphies to differentiate species of Sorex, however I found a number of autapomorphies for the species of *Sorex*. I

suggest that they be treated only as potential autapomorphies, but can provide a starting place for a more detailed investigation of the apomorphies of *Sorex*. Ideally, specimens of each species of *Sorex* need to be examined to find apomorphies to identify them to species.

There are few potential autapomorphies for species of *Blarina* (Table 2.10). There is a high degree of polymorphism within *Blarina* and this is makes it difficulty to differentiate species with autapomorphies. The internal temporal fossa is always large in *Blarina brevicauda* (22:1) but it is polymorphic for other *Blarina*; species other than *Blarina brevicauda* show all states.

Blarina carolinensis has two potential autapomorphies. Character 37 (shape of zygomatic process), is short (state 0) in *Blarina carolinensis* and wide (state 2) in other *Blarina*. The other autapomorphy is the posterior end of the zygomatic plate (40). This character shows state 1 in *Blarina carolinensis* and state 3 in other *Blarina*.

Character 7 is the only potential autapomorphy for *Blarina hylophaga*. It is not well supported because the character is polymorphic for other *Blarina*. There is not a single autapomorphy for this taxon in either the pruned PAUP tree or the composite tree.

The number and validity of species of *Cryptotis* is still uncertain; therefore, all proposed autapomorphies might change if more members are examined. The only autapomorphy for *Cryptotis goldmani* was character 1, teeth pigmentation. *Cryptotis goldmani* had darker pigment than other *Cryptotis*. However, pigmentation was highly polymorphic among all shrews and is poor character to use to differentiate taxa.

Character 17 is an autapomorphy for *Cryptotis magna* in the pruned PAUP tree and the composite tree but serves as a synapomorphy for *Cryptotis magna* plus *Blarina* in the full PAUP tree. *Cryptotis magna* is the only examined taxon within *Cryptotis* to have a reduced protoconal basin in M1 (31:0). The other *Cryptotis* are polymorphic for this

Table 2.10 Autapomorphies of some North American shrew species, * indicates ambiguity, ? indicates unknown state.

Taxon	**PAUP** (All Taxa)	**PAUP** (Pruned)	**Composite**
Blarina brevicauda	22: ? → 1	22: ? → 1	22: ? → 1
Blarina carolinensis	37: 2 → 0		37: 2 → 0*
	40: 3 → 1	40: 3 → 1	40: 3 → 1
Blarina hylophaga	7: ? → 1		
Cryptotis goldmani	1: ? → 1	1: ? → 1	1: ? → 1
Cryptotis magna		17: 0 → 1	17: 0 → 1
	31: 1 → 0		31: 1 → 0
		37: 0 → 2	37: 0 → 2*
Cryptotis mexicana	2: 2 → 1	2: 2 → 1	2: 2 → 1
	21: 2 → 0	21: 2 → 0*	21: 2 → 0
	26: 0 → 1	26: 0 → 1	26: 0 → 1
Cryptotis parva	9: 1 → 0	9: 1 → 0	9: 1 → 0
	10: 1 → 0	10: 1 → 0	
	20: 2 → 1	20: 2 → 1	20: 2 → 1
	23: 1 → 2		23: ? → 2
		32: 1 → 0	32: 1 → 0*
	35: 1 → 0		
		36: 2 → 1	36: ? → 1
		40: 3 → 1	40: 3 → 1
Megasorex gigas	5: ? → 1		5: ? → 1
	7: 0 → 1	7: 0 → 1	7: 0 → 1
	12: 0 → 1*	12: 0 → 1*	12: 0 → 1*
		34: 0 → 1	34: 0 → 1
Notiosorex crawfordi	1: 0 → 3	1: 0 → 3	1: 0 → 3
	5: ? → 2	5: 1 → 2	5: ? → 2
	12: 1 → 0*	12: 1 → 0*	12: 1 → 0*
	29: 0 → 1	29: 0 → 1	

character or have state 1. *Cryptotis magna* is also the only *Cryptotis* to have a wide zygomatic process (37:2), like *Blarina*.

Characters 2, 21, and 26 should serve to separate *Cryptotis mexicana* from the other *Cryptotis*. However, characters 2 and 26 are polymorphic in other *Cryptotis*. Only *Cryptotis mexicana* lacked a basin in the interarticular area among *Cryptotis*. My sample of *Cryptotis mexicana* was limited, and I was not able to examine any other members of the '*mexicana'* group besides *Cryptotis goldmani*.

Cryptotis parva shares many characters with *Blarina*, which are likely plesiomorphies from ancestral Blarinini. Characters 9, 10, and 35 could be plesiomorphic because the character states found in *Cryptotis parva* are also found in *Blarina*. This could complicate the identification of these taxa, and is especially significant because the ranges of *Blarina* and *Cryptotis parva* almost completely overlap. Character 23 is polymorphic in other *Cryptotis* and might not be an autapomorphy of *Cryptotis parva*. Characters 20, 36, and 40 are distinct from other *Cryptotis*. The ancestral state of character 20 is uncertain in the composite tree. State 1 of characters 36 and 40 are shared with *Sorex trowbridgii* and are not autapomorphies in the full PAUP tree.

Character 5 is a potential autapomorphy for *Megasorex gigas* because it differs from *Notiosorex crawfordi*, but the ancestral state is ambiguous. Character 7 was an autapomorphy in all trees examined. Character 12 could serve to separate *Megasorex gigas* from *Notiosorex crawfordi* because *Megasorex gigas* has more cusps on the talonid of m3, but given only two taxa I cannot reconstruct the ancestral condition for this character. *Megasorex gigas* also had more complex M3s (34) than *Notiosorex crawfordi*.

The teeth pigmentation in *Notiosorex crawfordi* is a unique autapomorphy. Only *Notiosorex crawfordi* had light teeth pigmentation among all taxa I examined. Characters 5, 12, and 29 are also potential autapomorphies.

Fossil identification using apomorphies

The three different trees in my analysis naturally will have different apomorphies (Figures 2.19 and 2.20). I considered a character to be a reliable apomorphy for identification if it was a synapomorphy or autapomorphy in both the composite molecular tree and in one of the PAUP trees. The reliable apomorphies are shown in Table 2.11. After each fossil specimen was scored in a character matrix, the scoring was then compared to Table 2.11 to match the characters present in the specimen to apomorphies that diagnose a particular taxon. This table greatly facilitates the comparison of character states present in specimens to synapomorphies and autapomorphies that can be used to diagnose the taxon.

The following taxa were identified previously from Hall's Cave: *Blarina carolinensis, Cryptotis parva, Notiosorex crawfordi, Sorex, Sorex cinereus, Sorex* cf. *haydeni,* and *Sorex cinereus or haydeni* [sic] (Toomey, 1993). I examined 47 dentaries or dentary fragments and 25 upper jaws. Some dentaries were complete, but only partial upper jaws were preserved. My identifications are summarized in Table 2.12. This table lists the original identifications in the column headings. The column *Sorex cinereus* / *cf haydeni* / *cinereus* or *haydeni* represents three individual specimens with those identifications. My identifications are listed in the left hand column, and were made to the most specific taxonomic level possible using on apomorphies. The full list of re-identified taxa is found in Appendix B.

I tested whether a few, key characters or autapomorphies could reliably identify taxa. However, due to intraspecific variation of many characters and that characters are autapomorphies only relative to sister taxa, I found that all available characters must be scored from each specimen to reliably identify specimens based on apomorphies. Some characters, long recognized to identify genera, such as the shape of the condyle (character

Table 2.11. Table of character states with apomorphies color-coded for all species examined.

TAXON	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Blarina brevicauda	1	0&1&2	0&1	0&2	3	0&1	0&1	1	1	0	1	1	1	1	0	1	1	1	1	2	1	1	0&1&2	0&1
Blarina carolinensis	1	0&1&2	0&1&2	0&1&2	2&3	0&1	0&1	1	0&1	0	1	0&1	0&1	0&1	0	1	1	1	1	2	1	0&1&2	1&2	1
Blarina hylophaga	1&2	0&1&2	0&1&2	0&1&2	3	0&1	0	1	0&1	0	1	0&1	1	1	0	1	1	1	1	2	1	0&1&2	1&2	1
Cryptotis parva	1&2	1&2	1&2	1&2	2	1	0&1	1	0	0	1	0	0&1	0&1	2	0	0	1	1	1	2	0&1	2	0&1
Cryptotis goldmani	1	2	1&2	1&2	1	1	0&1	1	1	1	1	1	1	0&1	2	1	0	1	1	2	2	0&1	1&2	0&1
Cryptotis magna	1&2	1&2	1	2	2	1	1	1	1	1	1	0	1	1	2	0	1	1	1	2	2	0&1	1&2	0&1
Cryptotis mexicana	2	1	1&2	1&3	1&2	1	1	1	1	1	1	1	0&1	0	2	1	0	1	1	2	0	0&1	2	0&1
Notiosorex crawfordi	3	0&1	0	0	2	0&1	0	0	1	1	0	0	0&1	0&1	1	0	2	1	0	1	0	1&2	0	0
Megasorex gigas	0	0	0	0	1	0&1	1	0	1	1	0	1	0&1	1	1	0	2	1	0	1	0	1&2	0	0
Sorex arcticus	2	3	2	2	1	1	0	1	1	1	1	1	0	0	0	1	0	0	2	0	0	0	1&2	0
Sorex bendirii	1&2	2	1	1	0	0	0	1	1	0	1	1	0	0	0	1	0	0	2	2	0	0	0	0
Sorex cinereus	2	3	2	2	0&1	0	0	1	1	1	1	1	0	0	0	1	0	0	1&2	0	0	0	0	0
Sorex fumeus	2	2	2	2	1	0	1	1	1	1	1	1	0	0	0	1	0	0	2	0&2	0	0	2	0
Sorex trowbridgii	2	2	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	0	2	2	0	0	1	1
Sorex vagrans	2	3	2	2	0&1	0&1	0	1	1	1	1	1	0	0	0	1	0	0	2	2	0	0&1	2	0
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40								
Blarina brevicauda	0&1	0&1	2	1	0&1	1	0&1	1	0	0&1	0	3	2	0	0	3						Synapomorphies		
Blarina carolinensis	1	0&1	2	1	0	1	1	1	0	0	0	3	0	0	0	1						Node 3		
Blarina hylophaga	1	0	2	1	0	1	0&1	1	0	0&1	0	3	2	0	0	3						*Blarinini*		
																						Blarina		
Cryptotis parva	1	0	1	0&1	1	2	0&1	0	0&1	0	0	1	0	0	0	1						*Cryptotis*		
Cryptotis goldmani	1	0	1	0	0	0&2	0&1	0&1	0	0&1	1	2	3	1	1	3						*Notiosoricini*		
Cryptotis magna	1	0&1	1	1	1	2	0	1	0	0	1	2	2	0&1	1	3						*Sorex*		
Cryptotis mexicana	1	1	1	0&1	1	2	1	1	0&1	0	1	2	3	1	1	3								
																						Autapomorphies	1	
Notiosorex crawfordi	0&1	0&1	0	0	1	2	0&1	0	1	0	2	?	1	0	0	2								
Megasorex gigas	?	1	0	0	0	2	1	0&1	1	1	2	?	1	0	0	2								
Sorex arcticus	0&1	0	3	0	0	2	1	0	0&1	1	1	2	3	0&1	0	0								
Sorex bendirii	0	0	3	0	1	2	1	0	1	1	0	2	3	1	0	0								
Sorex cinereus	1	0	3	0	0&1	0&2	1	0	0&1	1	1	1&2	0&3	0	0	0								
Sorex fumeus	0	0&1	3	0	0	2	1	0	0&1	1	1	1	0	0	0	0&2								
Sorex trowbridgii	1	0	3	0	1	2	1	0	0	1	1	1	0	0	0	1								
Sorex vagrans	1	0	3	0	1	2	1	0	0&1	1	1	1	0	0	0	0								

19) and the number of antemolars per upper jaw (character 27) were useful in determining which genera or tribe a specimen might belong (Jones and Manning, 1992; Carraway, 1995). These characters are synapomorphies, but more characters are needed to diagnose species.

A much smaller percentage of specimens were diagnosable to species as was originally described. Yet, I was able to diagnose more species of *Blarina*. I confirmed the presence of *Blarina carolinensis*, and based on autapomorphies identified *Blarina brevicauda* and *Blarina hylophaga*. However, the autapomorphies for *Blarina brevicauda* and *Blarina hylophaga* are weak. The identification of *Blarina brevicauda* is based on size if the internal temporal fossa (character 22), where state 2 (medium size) is fixed for *Blarina brevicauda* but varies in the other taxa, and the identification *Blarina hylophaga* is based on the upturning of the distal tip of the first lower incisor (i1, character 7), which is strong (7:0) in *Blarina hylophaga* but varies in the other *Blarina*.

Most of the specimens originally identified as *Cryptotis parva* preserve autapomorphies that can diagnose the specimens to the species level given the comparison species I examined. These characters were an anteroposteriorly reduced talonid of m1 (9:0), absent entocristids (10:0), in lateral view the upper articular condyle is short and the lower condyle is visible (20:1), and the canal into the temporal fossa is tiny (23:2). While I could not diagnose all specimens originally identified as *Cryptotis parva* to the species level, I could not identify any other species of *Cryptotis*.

When specimens of *Notiosorex* were originally identified, the only recognized extant species was *crawfordi*. Subsequently, several new extant and extinct species were named (Carraway, 2010) those species were recognized by cranial and dental measurements and molecular phylogenetics, rather than discrete morphologic phylogenetic characters. From published descriptions of the new species, I was unable to

discriminate species of *Notiosorex* using the characters in this study (Carraway and Timm, 2000; Baker, O'Neill, and McAliley, 2003; Carraway, 2010). Therefore, I have diagnosed the specimens from Hall's Cave as *Notiosorex*, but not to any species.

To identify the species of *Sorex*, Toomey used a dichotomous key to *Sorex* (Junge and Hoffman, 1981), and significant biogeographic assumptions to narrow the comparison species. He selected the extant species that are closest to the cave today (Toomey, 1993). In the absence of biogeographic assumptions, I could only diagnose specimens previously identified as *Sorex* to the genus level. No species-level identification was possible using apomorphic identification. Additionally, several specimens were so poorly preserved that they were not even diagnosable to Soricidae. There is a discrepancy in the species of *Sorex* listed in Toomey's dissertation and the catalog of the Vertebrate Paleontology Laboratory, Texas Natural Science Center (Toomey, 1993).

There are a number of distinct differences between the identifications I was able to make using apomorphies and the original identifications. While many specimens are diagnosable to the same or similar taxonomic level, some specimens cannot be diagnosed to the same taxonomic level using apomorphies. Some specimens were so fragmentary that I could not diagnose them to tribes, or even Soricidae. For example, TMM 41229-11048 was identified as *Blarina carolinensis*, but this is an edentulous upper jaw. I was unable to score any characters for this specimen and so could not even diagnose it to Soricidae. This was a rare occurrence, but of concern, because it is unclear what character or characters were used to identify this specimen as *Blarina*, let alone *Blarina carolinensis*. Specimens like this highlight the problem that occurs when there is a lack of description of how specimens were identified. This suggests that discrepancies of identification may be common both at Hall's Cave and at other Quaternary sites.

I was expecting that most of the specimens I would examine would be relatively complete, but not diagnosable to the species level. Several specimens were relatively complete but lacked clear synapomorphies and autapomorphies to provide a species level diagnosis. For example, TMM 41229-11084 was identified originally as *Blarina carolinensis*. The posterior extent of the alveolus of the lower incisor in labial view of this specimen is like *Cryptotis parva* (character 5:2) as is the articular condyle in labial view (character 20:1). However, the talonid of m1 and m2 are like Blarina (character 9:1), as is the lingual side of the interarticular area (character 21:1) and the canal in the temporal fossa (character 23:1). This is an unclear combination of characters leads to a diagnosis of Blarinini for this specimen. Another example is TMM 41229-10817 that was identified was *Cryptotis parva*. The talonid of m1 and m2 is anteroposteriorly reduced relative to the trigonid (character 9:0), and the entocristids are absent from m1 and m2 (character 10:1). These are relative autapomorphies for *Cryptotis parva*, and these states are also found in *Blarina*. Character 23, the canal into the temporal fossa is present and well developed (23:1). This is not found in *Cryptotis parva*, but is found in *Blarina*. There are no other morphologies preserved in this specimen that are apomorphies for either *Cryptotis* or *Blarina*, but it can be diagnosed to Blarinini.

Surprisingly, many fragmentary specimens still preserved apomorphies that allowed for genus and species-level diagnoses (Table 2.11). One example is TMM 41229-12048. It has a single autapomorphy but this allows it to be diagnosed to *Cryptotis parva*. The posterior border of P4, M1, and M2 is strongly emarginated (32:0) in *Cryptotis parva*, and this is not found in any other Blarinini taxa.

Some specimens were also originally miss-identified. For example, TMM 41229-7016 was identified originally as *Cryptotis parva*, but has a number of apomorphies that diagnose it as *Notiosorex*. Additionally, TMM 41229-11670 may have been identified

originally as *Notiosorex crawfordi* because it is missing the fourth upper antemolar, the state found in *Cryptotis*. However, the alveolus for this tooth is present and other apomorphies support the identification that this specimen is *Cryptotis parva*.

Overall, there were fewer specimens identifiable to refined taxonomic levels (genus or species) based on apomorphies, than with the original identification methods (Table 2.12). Only 5 of 29 specimens (17%) of *Blarina* were identified to the species level. However, 21 of 29 (72%) were identified to genus and/or species. For *Cryptotis parva*, 9 of 13 (69%) specimens were identified to the species level. This higher percentage probably reflects the greater number of autapomorphies that separate *Cryptotis parva* from the other *Cryptotis*. I did not refer any specimens of *Notiosorex* to species, but 17 of 24 specimens (71%) originally identified as *Notiosorex crawfordi* could be assigned to *Notiosorex*.

Conclusions

There are challenges to all identifications. Whether specimens are identified based on soft tissue characters such as pelage or ear length, skeletal characters such as the shape of the zygomatic process, or from the similarity of genetic material, there are always basic assumptions that underlie the techniques. Fossils can be more difficult to identify than specimens collected in the field today because fossils often consist of only skeletal remains that are disarticulated, fragmentary, and chemically altered. Therefore, it is imperative to be clear about which criteria are used to identify fossils.

By examining in a phylogenetic context most of the characteristics used to identify fossil shrews in North America, I described both the variation that exists within and between selected shrew taxa, and provided a solid basis to examine the phylogeny of

shrews based on morphology. This is an important first step towards understanding how morphology changed throughout the evolution of Soricidae.

Table 2.12. Summary of the number of specimens identified from Hall's Cave Pit 1E. Column headings list the original identifications (Toomey, 1993). Rows list identifications made in this study. ? indicates that the specimen could not be diagnosed.

	Blarina carolinensis	*Cryptotis parva*	*Notiosorex crawfordi*	*Sorex*	*Sorex cinereus/ cf haydeni/ cinereus or haydeni*	Sum
Blarina	16					16
Blarina brevicauda	1					1
Blarina carolinensis	2					2
Blarina hylophaga	2					2
Blarinini	6	2				8
Cryptotis parva		9	2			11
Cryptotis		1				1
Node 3	1					1
Notiosorex		1	17			18
Notiosoricini			4			4
Sorex				1	3	2
Soricidae			1	2		3
?	1			1		2
Total specimens	29	13	24	4	3	73

I present a significant study of comparative morphology of many North American shrews. The enhanced understanding of morphology and variation of shrews will impact the identification of shrew taxa from the fossil record. I chose to include photographs of all character states for two reasons. First, it will eliminate much of the ambiguity of purely written character descriptions. Second, photographs are tied to specific museum

specimens that can be re-examined if questions exist about alternate interpretation of characters.

The impetus for writing this paper was to explore the implications of identifying North American shrews using apomorphic characters from the dentition, skull, and mandible, and to test the validity and broader applicability of previously established characters that were used to differentiate local or regional assemblages of shrews. An underappreciated challenge to accurate and reliable identifications is a realistic understanding of intraspecific and interspecific variation. I have tried to document the variation I observed and considered this when making identifications. It is likely that if intraspecific and interspecific variation are ignored the ability to identify species are likely to be overstated. This is true regardless of the methodology used to identify specimens.

If gross similarity is used to identify fossils, I would suggest that the exact characteristics and the geographic and temporal range of the comparison pool of species used for the identification be explicitly included in a published description. It is especially important to note if geographic assumptions are part of the identification because these will bias any subsequent interpretations about range shifts. For example, when characteristics for identification of lagomorphs were examined with an approach intended to minimize geographic and temporal assumptions individual species of *Ochotona*, *Sylvilagus*, or *Lepus* were not identified (Jass, 2009). Similarly, the examination of *Microtus* specimens from Irvington, California showed that species-level identifications were not possible when comparisons were made to specimens from a broad geographic range (Bell and Bever, 2006).

In comparison to the original identifications, using apomorphies to identify shrews improved the identifications by having a specific assemblage of apomorphic characters that can be assessed by later authors, and I have documented the methodology

I used as well. An added advantage of using apomorphies to identify the shrews from Hall's Cave was that this technique increased the total number of species of shrews identified. There were a greater number of species of *Blarina* identified. However, as previously discussed, the autapomorphies that diagnose *Blarina brevicauda* and *Blarina hylophaga* are weak. For some specimens, the species of *Blarina* could not be diagnosed, but the lack of autapomorphies suggests that those taxa were not *Blarina carolinensis*. Even in this case, the number of recognized species increases based on apomorphies because there is *Blarina carolinensis* as well as an additional species of *Blarina*, either *Blarina brevicauda*, *Blarina hylophaga*, or potentially an unrecognized extinct species.

A distinct advantage of the apomorphic identification methodology is that identifications are based on specific character states. If the morphology is preserved on a specimen, then characters can diagnose a specimen from family to tribe, genus, or species, and the identification is justified by specific apomorphies. The advantage of apomorphic identifications is that each of the characters are interpreted in phylogenetic context. By basing identifications on apomorphies, the synapomorphies identify the specimen to higher taxonomic levels simultaneously. Other methodologies such as taxonomic keys, morphometrics, or gross similarity can identify species, but higher taxonomic levels are then inferred. If a taxonomic key or the discriminant function from a morphometric analysis fails to identify a specimen, those systems are not designed to place the specimen in a taxonomic hierarchy. This is especially true if there are multiple species from the same genus. Apomorphies can refine identifications below the genus level even if species cannot be determined by placing the specimen within a clade within the genus. This is not usually possible in other systems because they are not based on a phylogeny.

It is important to score all characters of a specimen. If the relationships within a clade change then different characters may become apomorphies. However, the character states assigned to a specimen would not change. If future workers have the character matrix for each specimen then apomorphic identifications can be re-interpreted quickly. Apomorphies are always relative to the phylogenetic tree on which they are based. While it is likely that future phylogenetic analyses may produce different hypotheses of the relationships of the taxa in this study, it is a much simpler task to re-interpret apomorphies based on new trees than having to rescore each specimen.

If apomorphic identification is widely adopted to identify Quaternary fossil mammals, it may reduce taxonomic resolution for many taxa. As I found at Hall's Cave, using apomorphies to identify the shrews resulted in a reduction in the number of specimens identified to the species level. Many of the specimens originally identified to species should not have been. The original identifications were based on morphology and then refined to species by utilizing geography to narrow the choice of comparison species. This was a significant problem for *Blarina*, but less so for *Cryptotis* and *Notiosorex*. Two species of *Blarina*, *Blarina carolinensis* and *Blarina hylophaga*, are found in Texas today, and the range of both is close to equidistant from Hall's Cave. There is no justification provided for why *Blarina carolinensis*, rather than *Blarina hylophaga*, was identified (Toomey, 1993). The assumption that there was one species of *Blarina* made it less likely that any other species could be recognized.

I did not find any other species of *Cryptotis* aside from *Cryptotis parva*. This may indicate that there is a significant barrier to dispersal that prevents any other species of *Cryptotis* from moving as far north as Hall's Cave anytime during the last 20,000 years. The present range of *Cryptotis parva* is from southern Canada in the north to Mexico in the south. No other extant species of *Cryptotis* is found north of Mexico. The

biogeographic factors that influence the distribution of *Cryptotis* is an area for future research.

Any speciose group of small mammals (like *Sorex* or *Cryptotis*) could be extraordinarily difficult or impossible to identify to the species level using apomorphies. Apomorphies are poorly understood and largely unexplored in most small mammal groups. It is possible that detailed study of morphology could yield additional characters that might resolve species-identifications, but it is likely that some reduced taxonomic resolution is inevitable if fossils are identified without temporal and geographic assumptions.

Although using apomorphies to identify shrews did increase the number of species recognized from Hall's Cave, there were fewer specimens identifiable to species. Therefore, I would advise restraint in using the Hall's Cave data set for making certain types of paleoecologic interpretations about the small mammals. First, some caution must be used if interpreting the range shifts of shrews from the Pleistocene to the present because geography was used in the original identifications. Second, because the number of specimens that can be identified to species may be less than originally described any analysis of the relative abundance of shrew species through time would have to be re-assessed. These results could certainly impact interpretations made using other fossils of similar age from other Quaternary sites that were identified using a similar method to that of Hall's Cave.

The widespread application of apomorphic identification for the identification of small mammals is likely to have profound effects. Shrews have a number of distinct morphologies of the teeth and upper and lower jaws that provide characters that can be interpreted phylogenetically. It is a challenging and time consuming process to code morphology as phylogenetic characters. If apomorphic identification is to be adopted for

the identification of other small mammals, a concerted effort is necessary to expand the morphological dataset of phylogenetic characters in order to have enough characters to identify individual species.

CHAPTER 3: PROBLEMATIC FAUNA-BASED PALEOECOLOGIC APPROACHES: WHY SPECIES-RICHNESS MODELS AND CENOGRAMS FAIL

ABSTRACT

I used the fauna from Hall's Cave to test species-richness models and cenograms for internal consistencies, consistent reconstruction between these two paleoenvironmental approaches, and the ability of both approaches to recover similar paleoenvironmental conditions as independent paleoenvironmental proxies. There are a number of independent paleoenvironmental proxies from the region near Hall's Cave, including pollen, soil carbonate isotopes, magnetic resistivity, and speleothem growth rates. Species-richness models use the extant biota to establish linear correlations between the numbers of species of groups of mammals and the mean annual temperature and precipitation of a geographic region. Species-richness models are sensitive to any bias associated with how species are identified. Any change in the number of species will alter the paleoclimatic results generated by the models. A cenogram is a plot of $\log_{10}$ body mass from largest to smallest mammals that is reported to be useful for the interpretation of the paleoenvironment of a fossil deposit. Cenograms cannot reliably be quantified, and that allows for almost any interpretation about past environment to be made from a cenogram drawn from a paleontological fauna. Neither species-richness models nor cenograms agree with paleoenvironmental reconstructions based on proxy data from the Late Pleistocene and Holocene. Cenograms and species-richness models are unreliable and fraught with intractable problems. Both approaches should be abandoned as tools for paleoecological reconstruction.

INTRODUCTION

Paleoenvironmental interpretations based on mammals

In the latter-half of the nineteenth century, paleontologists recognized that the post-Pliocene mammalian fauna differed appreciably from the mammal species of the preceding epochs (e.g., Cope, 1871). It was also noted that many Quaternary fossils were similar to or indistinguishable from extant species, and that although the fossils were similar to extant species, they could be found in different geographic regions than they are today (Brown, 1908). Two major sources of evidence that Pleistocene climate was different than the present were evidence of widespread continental glaciation in the northern hemisphere and the presence of extralimital species in Pleistocene faunas.

> For example, the occurrence in Pleistocene times… of such arctic types as the walrus in Virginia and South Carolina along the Atlantic coast, the musk ox in Pennsylvania, West Virginia, Kentucky, Indian Territory and Iowa, and the reindeer in New Jersey, Pennsylvania, Kentucky and Iowa, certainly shows that an arctic climate once reached far to the south (Adams, 1905).

The relationship of mammals to climate was recognized as an important factor controlling the geographic distribution of mammalian faunas. It was argued by Cope (1871), that the onset of glaciation altered the composition of the pre-Quaternary fauna, and that the retreat of the continental glaciers opened new environments that could be occupied by mammals dispersing from tropics. At the time, there was a concerted effort by biologists and paleontologists to resolve the factors that influenced the present ranges of all species of plants and animals. It was recognized that the conditions of the present environment were not the only characteristics controlling the distribution of terrestrial species, but it was the cumulative result of many factors, including the succession of glacial and interglacial climates (e.g., Adams, 1905). However, in the pre-plate tectonics view of the earth, ocean basins were thought to be static, and climate change was

hypothesized to be the principal factor influencing the distribution of species (Matthew, 1915). It was advocated by Matthew (1915) that it was the environment that "migrated" and that "primitive species" dispersed with it. It was only when species did not disperse that they adapted to new environments.

By the middle of the twentieth century, it was thought that most terrestrial species of plants and animals originated in the Pliocene or earlier and that environmental changes in the Pleistocene accounted for the present day distribution of the biota (Deevey, 1949). Much of the focus of research on the relationship between mammals and climate shifted from a focus on determining the cause of the present distribution of mammals to using various groups of mammals to make paleoenvironmental interpretations of Quaternary deposits. For example, insectivorans (Hibbard, 1953; Graham and Semken, 1976), rodents (Graham, 1984; Hadly, 1997), and small mammals collectively (Guilday et al., 1964; Grayson, 1987; Winkler, 1990) were used to describe in general terms how the paleoenvironment was warmer or cooler, or wetter or drier from the present because of the presence or absence of certain mammal taxa. These were qualitative comparisons of a Quaternary fauna to other Quaternary faunas or to modern faunas.

Two methods attempt to go beyond generalized description of the paleoenvironment using mammalian faunas. The first of these were cenograms and second to be developed were species-richness models. These two paleoenvironmental approaches were developed to use only species of mammals to reconstruct particular past environments (cenograms), or yield precise climatic values for temperature and precipitation (species-richness models). I carefully examined the claim that both approaches accurately reconstruct past environments using fossil mammals.

Background

Species-richness models

Species-richness models were developed from the observation that there are significant correlations between the extant biota and temperature and precipitation. It was hypothesized that these correlations could be used to reconstruct past environmental conditions. The species richness models described by Montuire et al. (1997) used the relationship between the numbers of species of an extant group of mammals and temperature or precipitation of a geographic region. They found a simple, linear correlation between the numbers of species of a group of mammals from a location and temperature or precipitation. The plots are simple bivariate graphs with the number of species on the x-axis and the climatic variable on the y-axis. Those graphs are a model that can predict temperature or precipitation when the number of species of a group of extant mammals is known. It was hypothesized by Montuire et al. (1997) that these models could be used to predict past temperature and precipitation based on the number of species of a group of mammals from fossil sites. In this context, a fossil site may be a single deposit that was excavated as one stratigraphic unit, or a site may encompass any number of individual excavation units that represent discrete time intervals and would be interpreted separately.

The first species-richness model developed by Montuire et al. (1997) used the number of species of extant arvicoline rodents (voles and lemmings) found at a location plotted against mean annual temperature, mean temperature of the coldest month, and mean temperature of the warmest month of the location (Montuire et al., 1997). In the description of the methodology, the exact criterion used to define locations was not described, only that they were drawn from "a database on extant local faunas" (Montuire et al., 1997:188). Those localities ranged in area from 100 km^2 to 10,000 km^2. More

explicit description of localities was provided by Ruez (2007) in his attempt to improve the models. To better control for geographic variation, Ruez based his localities on the ecoregions of the United States and Canada from Ricketts et al. (1999). Ecoregions are defined by similar floral, faunal, and environmental features of an area.

In the model developed by Montuire et al. (1997), the number of species and climatic parameters from a large number of locations were plotted, and then a least squares linear regression and R^2 value were calculated. The ultimate goal of Montuire et al. (1997) was, using their models, to take the number of species of a group of mammals from a paleontological locality, and use the equation of the regression line generated from the plot of modern localities to calculate the temperature or precipitation of each depositional unit at a paleontological locality. Their idea was that someone could potentially take the number of arvicoline species from any depositional unit and calculate the mean annual temperature, mean temperature of the coldest month, and mean temperature of the warmest month of the location from the time when the deposit was formed using their models.

In subsequent publications, this method was applied to Old World murines (Aguilar et al., 1999) and sigmodontine rodents (Legendre et al., 2005). These models were originally used to interpret the paleoenvironment of Plio-Pleistocene sites in Europe, but now have been applied to sites as old as Miocene (Montuire et al., 2006), and as far removed as south-east Asia (Tougard and Montuire, 2006). Subsequently, more models were tested to determine the utility of different species of rodents, insectivorans, artiodactyls, carnivorans, chiropterans, and other groups of mammals in North America to generate meaningful temperature and precipitation correlations (Ruez, 2007).

The model developed by Montuire et al. (1997) was only superficially tested using independent climate proxies. The only test was a comparison of the temperature results

from several paleontological sites in Europe to a synthetic isotopic curve from the last 100,000 years that was published by Martinson et al. (1987). The test failed. It was acknowledged by Montuire et al. (1997) that the data from fossil sites did not match the isotope curve. They proposed that more analysis was needed (Montuire et al., 1997). However, there have been only limited tests of this methodology and subsequent authors have used the same methods (Montuire et al., 1997) to attempt to find correlations between other mammals and environment. Another model was developed by several of the same authors (Montuire et al., 1997) using sigmodontine rodents and mean annual temperature, minimum temperature, maximum temperature, and annual precipitation (Legendre et al., 2005).

Significant modifications to species-richness models were implemented by Ruez (2007). He made an explicit attempt to avoid overlap between localities and to encompass as much ecological disparity as possible so that the correlation statistics generated from the localities would not have artificially inflated values not related to natural processes. To ensure maximum variation, localities were selected from ecoregion maps (sensu Ricketts et al., 1999). Two locations within each of the ecoregions of the United States and Canada were selected, and then faunal lists and climatic data were compiled from published resources (Ruez, 2007).

Ruez created additional species-richness models for a number of different groups of mammals and correlated them with maximum, minimum, mean annual temperature, and precipitation. In the models developed by Ruez (2007), the strongest correlations predicting mean annual temperature were with Sigmodontinae, Chiroptera, Arvicolinae, the total number of mammal species, and the small mammals (which he defined as Insectivora + Lagomorpha + Rodentia). The best predictors of precipitation were

Insectivora, Artiodactyla, large mammals (which he defined as Carnivora and Artiodactyla), and Rodentia.

Cenograms

Cenograms originally were developed to examine modern ecosystems and to explain predator-prey relationships (Valverde, 1964), but were adapted later as a paleoenvironmental approach (Legendre, 1986). A cenogram is a plot of $\log_{10}$ body mass from largest to smallest mammal excluding the bats and carnivorans (Legendre, 1986). A number of cenograms of modern sites, primarily from Africa and Europe, were developed by various authors as frames of reference for comparison to paleontological sites (Legendre, 1986; Gingerich, 1989; Travouillon and Legendre, 2009). The operational assumption is that if the cenogram from a paleontological site is similar to the cenogram generated from a modern location then the environments of both sites are similar. Cenograms were used by Legendre (1986) as a paleoenvironmental indicator to make interpretations on Late Eocene and Oligocene sites in France. There was no test of their applicability to a broad range of modern sites or to younger fossil deposits reported by Legendre (1986). Subsequently, cenograms were used primarily as a paleoenvironmental tool for interpreting Tertiary sites (e.g., Gingerich, 1989; Gunnell, 1994), but were applied to sites of different ages all over the world using the same modern environmental reference frame to make interpretations (e.g., Croft, 2001; Travouillon et al., 2009).

The standard interpretation of cenograms is based on the shape of three parts of the graph (Fig. 3.1). A cenogram is a plot of $\log_{10}$ body mass of the mammals from a locality plotted in order from largest to smallest. The shape of the plot is hypothesized to correlate with aspects of modern environments (Legendre, 1986). The large mammals are plotted on the left of the graph. The slope of large mammals is hypothesized to

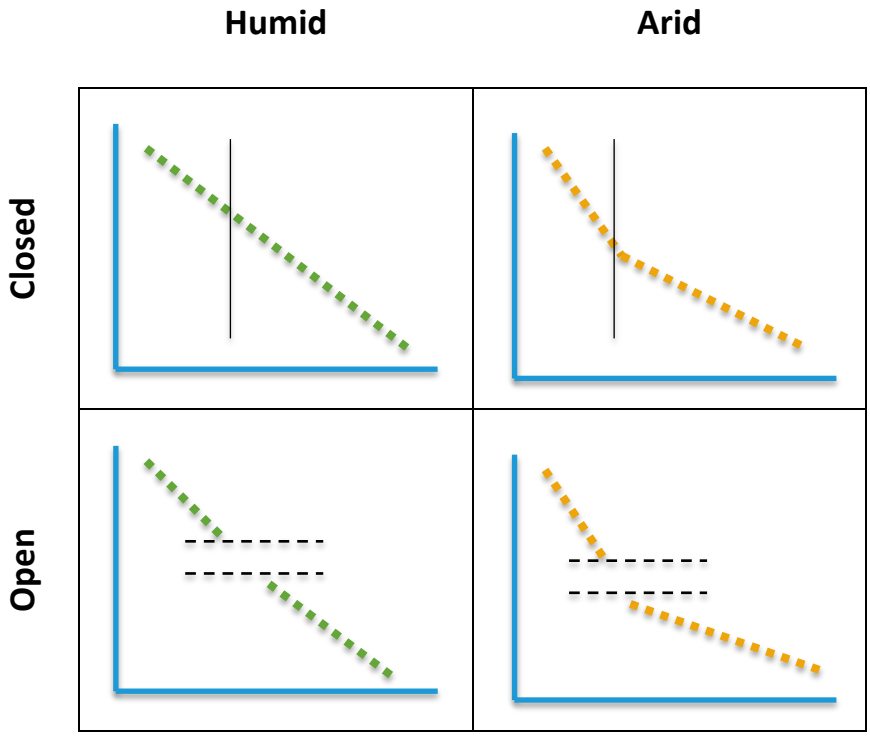


Figure 3.1. The standard interpretations of cenograms based on Travouillon and Legendre (2009). The dots represent individual species plotted from left to right in decreasing size. To the left of the vertical line are the large mammals. The slope of the large mammals was proposed to indicate moisture; the steeper the slope the more arid the environment. The black horizontal dashed lines indicate a gap between large and small mammals. If there is no gap between large and small mammals then the environment is hypothesized to have a closed canopy. If there is a gap, this is interpreted to be an open canopy.

indicate relative moisture, with a steeper slope interpreted to indicate a more arid environment. The slope of the body mass of small mammals is suggested to reflect temperature, with a steeper slope interpreted to indicate colder temperatures (Legendre, 1986). Finally, if there is a 'gap' or 'offset' between the medium sized mammals (8 kg to 0.50 kg), it is interpreted to indicate an open-canopy habitat (Travouillon and Legendre, 2009).

Though an average slope of the small and medium mammals on the cenograms for modern Old World environments was presented by Gingerich (1989), further attempts to quantify cenograms were unsuccessful (Rodrigues, 1999). It was shown by Rodrigues (1999) that there is no quantitative relationship between environment and the slope of cenograms. In response to the failure of cenograms to yield a statistically significant relationship to temperature or aridity (Rodrigues, 1999), it was re-emphasized that interpretations should only be made by visual inspection, not any quantification of slope, or 'amount of gap' (Travouillon and Legendre, 2009).

Testing species-richness models and cenograms

It was my expectation that both species-richness models and cenograms would be useful for reconstructing past environments from Quaternary sites. I first sought to test the reliability of species-richness models and cenograms to reconstruct the paleoenvironment from an area with a number of independent paleoenvironmental proxies that agree. Even though the interpretations of cenograms are based on correlations to modern mammals, they have never been tested on Quaternary sites. That would provide a reasonable test of the reliability of cenograms if the Quaternary sites had the same or closely related species to the cenograms from modern environments that

were used for interpreting the paleoenvironment of paleontological sites. I felt it was essential to test species-richness models on a single, well-preserved Quaternary deposit that has multiple independent proxies. Independent paleoenvironmental proxies are necessary to determine if the approaches can reconstruct paleoenvironment in a manner consistent with established physical and chemical proxies.

My tests revealed a number of potential problems with the reliability and predictions of species-richness models and cenograms when compared to paleoenvironmental proxies that are not based upon mammals. Some problems result from difficulties with the basic methodology, and some from flawed assumptions about the relationship between mammals and climate. Here, I discuss the methodological problems with these approaches, and demonstrate that they are inconsistent with paleoenvironmental techniques that are independent from the fauna. I tested the approaches using a well-studied faunal sequence that spans the Late Pleistocene and Holocene, Hall's Cave.

MATERIAL AND METHODS

Hall's Cave sequence

Hall's Cave is located on the Edwards Plateau in northwestern, Kerr County, Texas. The cave was excavated in arbitrary five-centimeter levels, and over one hundred radiocarbon dates were taken from the site (Toomey, 1993; Cooke, 2005). Materials from this excavation are ideal for discerning relatively short-term changes in the mammal fauna through time. The well-controlled stratigraphy, good chronology, and the number of other independent paleoenvironmental proxies for the Edwards Plateau, make Hall's

Cave an ideal site for testing the ability of the species-richness models and cenograms to reconstruct paleoenvironmental parameters.

Species-richness models

I expanded the number of species-richness models developed by Ruez (2007) by testing more sophisticated measures of climate than merely temperature and precipitation. I hypothesized that seasonality (differences in monthly mean temperature) or frost-free days could have a greater correlation with the number of mammal species. I created species-richness models for the number of frost-free days, the maximum difference in mean monthly temperature, average difference in mean monthly temperature, and maximum difference in mean monthly high temperature against the number of species of total terrestrial mammals, small mammals, insectivorans (shrews and moles), and arvicolines (sensu Wilson and Reeder, 1993 for all taxa). I utilized the same two locations from each of the ecoregions of the United States and Canada, and the same faunal lists and climatic data compiled by Ruez (2007). For each model, the number of species of each group of mammals was plotted against the climatic parameters, and then a least squares linear regression and R^2 value were calculated.

To test species-richness models for internal consistency, consistency between the models, and correlation with independent paleoenvironmental proxies I used the models developed by Ruez (2007) and by Legendre et al. (2005), and applied them to the published list of species for each excavation level of Hall's Cave (Toomey, 1993). Many specimens were identified to species, but other fossils were identified to various taxonomic levels by Toomey (1993). Some taxa, such as *Reithrodontomys* and *Peromyscus* were identified as *Reithrodontomys* sp. or *Peromyscus* sp. For the taxa that

were only identified to genus, I counted them as a single species. This is a conservative estimation of diversity, but justifiable given that there is no other evidence to suggest how many other species may be present based solely on morphology. A third group of fossils was identified by Toomey (1993) to genus and then was listed as either two or more species. Those taxa were counted as a single species as well.

I calculated the total number of species of total mammals, large mammals, small mammals, bats, insectivorans, rodents, sigmodontines, arvicolines, carnivorans, and artiodactyls for each excavation level, following the higher-order taxonomy used by Wilson and Reeder (1993). Hall's Cave was excavated by 5 cm levels (Toomey, 1993), and each level was treated as an excavation unit. Using the number of species for each group of mammals, I then calculated temperature and precipitation values based on the equations derived by Ruez (2007) and Legendre et al. (2005) for the each level in Hall's Cave.

To test the effect of specimen identification on these models, I compared the mean annual temperature estimates I generated from the sigmodontine models to temperature estimates generated if the same number of species was identified as are found in Texas today. There are significantly more extant species because most of the specimens of sigmodontines were identified only to generic level (Toomey, 1993), and I counted them as a single species.

I then compared the temperature and precipitation values estimated from the species richness models developed by Ruez (2007) and Legendre et al. (2005) to independent paleoenvironmental proxies. The proxies used were derived from C^{13} isotopes (Nordt et al., 1994), speleothems (Musgrove et al., 2001), sedimentology (Cooke, 2005), magnetic susceptibility (Ellwood and Gose, 2006), and pollen (Boulter et al., 2010).

Cenograms

I generated a cenogram for the mammals found historically near Hall's Cave, based on the county records for Kerr County (Schmidly, 2004). That cenogram provides a baseline for the interpretation of the cenograms generated from paleontological data. I generated cenograms for four levels of the Hall's Cave section. The four levels were 60-65 cm, 120-125 cm, 145-150 cm, and 210-215 cm of the deposit. These correspond to four time intervals, 5, 10, 12, and 15 ka, respectively. I selected those levels because they contain specimens dated to the time intervals from the most recently published radiocarbon dates (Cooke, 2005). I accepted the species as listed by Toomey (1993) following the same procedure as for the species diversity-indices. Body mass data for all taxa came from Ecological Archives E084-094 (Smith et al., 2003).

I then tested the cenograms from Hall's Cave in several ways. I first tested whether the number of identified species affected the interpretations. *Geomys*, *Thomomys*, *Cratogeomys*, *Neotoma*, *Peromyscus*, and *Reithrodontomys* are speciose genera of rodents. Those taxa were only identified to genera by Toomey (1993). To test the effect of taxonomic assumptions, I compared the difference in the shape of cenograms with all the species of *Geomys*, *Thomomys*, *Cratogeomys*, *Neotoma*, *Peromyscus*, and *Reithrodontomys* from Texas plotted individually, and as a single datum point with an average mass of all species of a genus. I then examined the suggestion that purely qualitative comparisons between cenograms should be used to make interpretations. I tested this by drawing one cenogram from Hall's Cave with two different dimensions, and compared it to the cenograms from modern environments. Finally, I compared the paleoenvironmental signal of cenograms to the species-richness models, and to independent proxies.

RESULTS

Species-richness models

The results of my analysis of seasonality and frost-free days for the extant biota yielded no significant correlations to the number of species of any group of mammals. The models I developed for the number of frost-free days, the maximum difference in mean monthly temperature, average difference in mean monthly temperature, and maximum difference in mean monthly high temperature for the number of species of total terrestrial mammals, small mammals, insectivorans (shrews and moles), and arvicolines showed a maximum correlation coefficient of 0.28, and several had correlation coefficients that approached zero (Tables 3.1, 3.2, 3.3, and 3.4).

Table 3.1. Results of the regression of the plot of frost-free days.

Taxon/group	Equation of regression line	R^2
Total terrestrial mammals	y = -1.8581x + 300.31	$R^2 = 0.038$
Small mammals	y = -4.6416x + 317.32	$R^2 = 0.086$
Insectivorans	y = 0.2035x + 204.29	$R^2 = 2.4x10^{-5}$
Arvicolines	y = -3.1193x + 216.69	$R^2 = 0.0066$

Table 3.2. Results of the regression of the plot of the maximum difference in mean monthly temperature.

Taxon/group	Equation of regression line	R^2
Total terrestrial mammals	y = 0.7925x + 20.551	$R^2 = 0.28$
Small mammals	y = 1.035x + 36.453	$R^2 = 0.154$
Insectivorans	y = -1.2116x + 66.25	$R^2 = 0.02827$
Arvicolines	y = 2.003x + 54.693	$R^2 = 0.10438$

Table 3.3. Results of the regression of the plot of average difference in mean annual temperature.

Taxon/group	Equation of regression line	R^2
Total terrestrial mammals	y = 0.2742x + 9.3329	$R^2 = 0.23$
Small mammals	y = 0.4798x + 11.868	$R^2 = 0.23$
Insectivorans	y = -0.7687x + 26.46	$R^2 = 0.080$
Arvicolines	y = 0.0669x + 23.331	$R^2 = 0.00081$

Table 3.4. Results of the regression of the plot of maximum difference in mean monthly high temperature.

Taxon/group	Equation of regression line	R^2
Total terrestrial mammals	y = 0.6005x + 10.293	$R^2 = 0.18417$
Small mammals	y = 0.8091x + 21.735	$R^2 = 0.10842$
Insectivorans	y = -0.0157x + 41.519	$R^2 = 5.5x10^{-6}$
Arvicolines	y = 2.6808x + 32.101	$R^2 = 0.21541$

There was a slight negative trend to the total terrestrial mammals (Fig. 3.2) and small mammals for the frost-free days (Fig. 3.3). Plots of frost free days for insectivorans (Fig. 3.4) and arvicolines (Fig. 3.5) showed essentially no correlation.

There was a slight positive trend for the number of species of total terrestrial mammals (Fig. 3.6), small mammals (Fig. 3.7), and insectivorans (Fig. 3.8) and average difference in mean monthly temperature, but the correlation was not significant. There was almost no correlation for arvicolines and average difference in mean monthly temperature (Fig. 3.9).

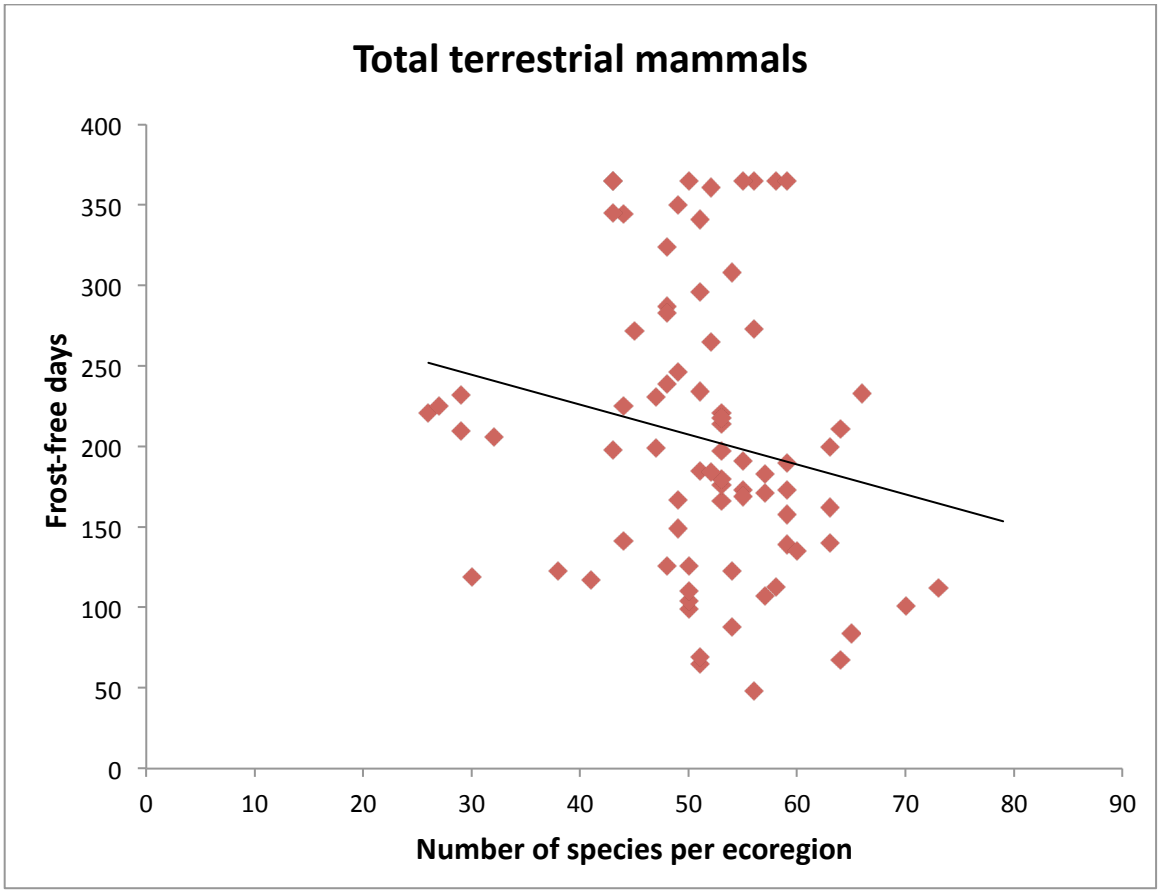


Figure 3.2. Plot of the number of species of total terrestrial mammals against the number of frost-free days per ecoregion.

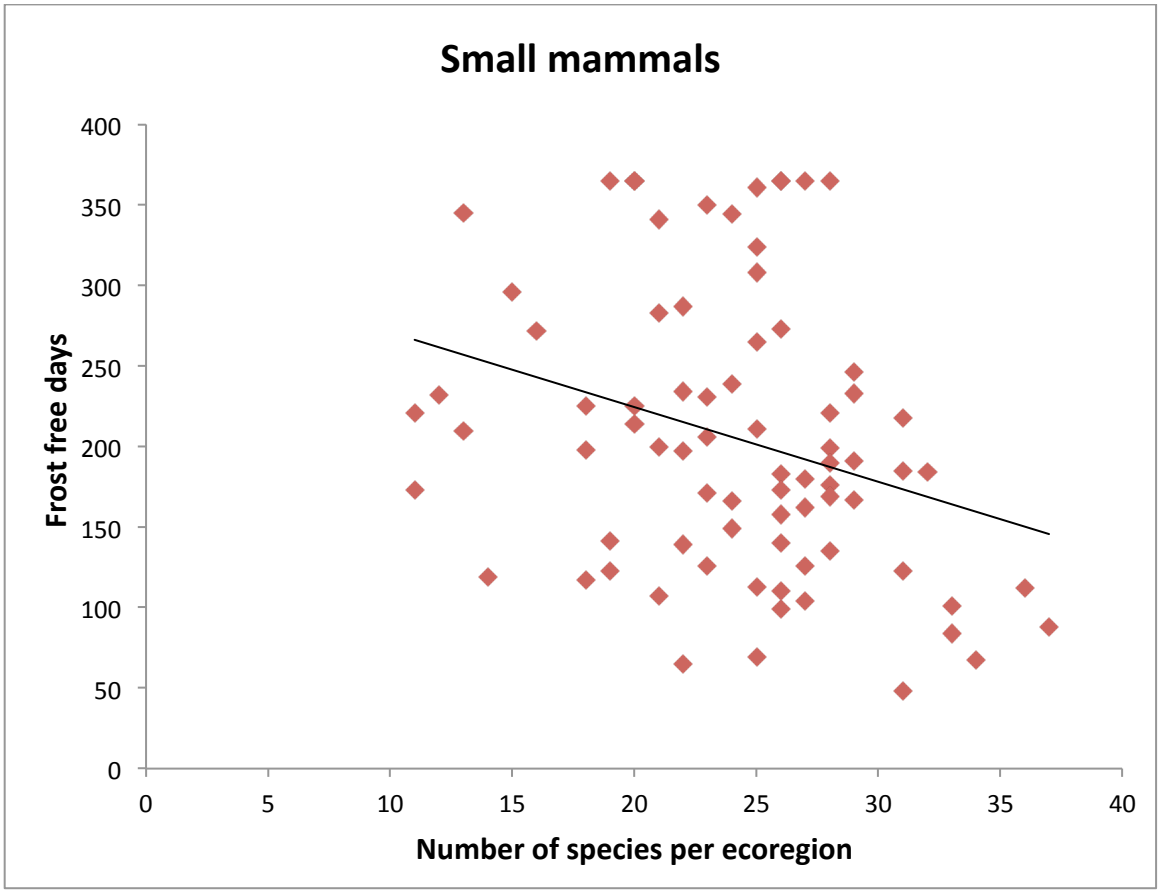


Figure 3.3. Plot of the number of species of small mammals against the number of frost-free days per ecoregion.

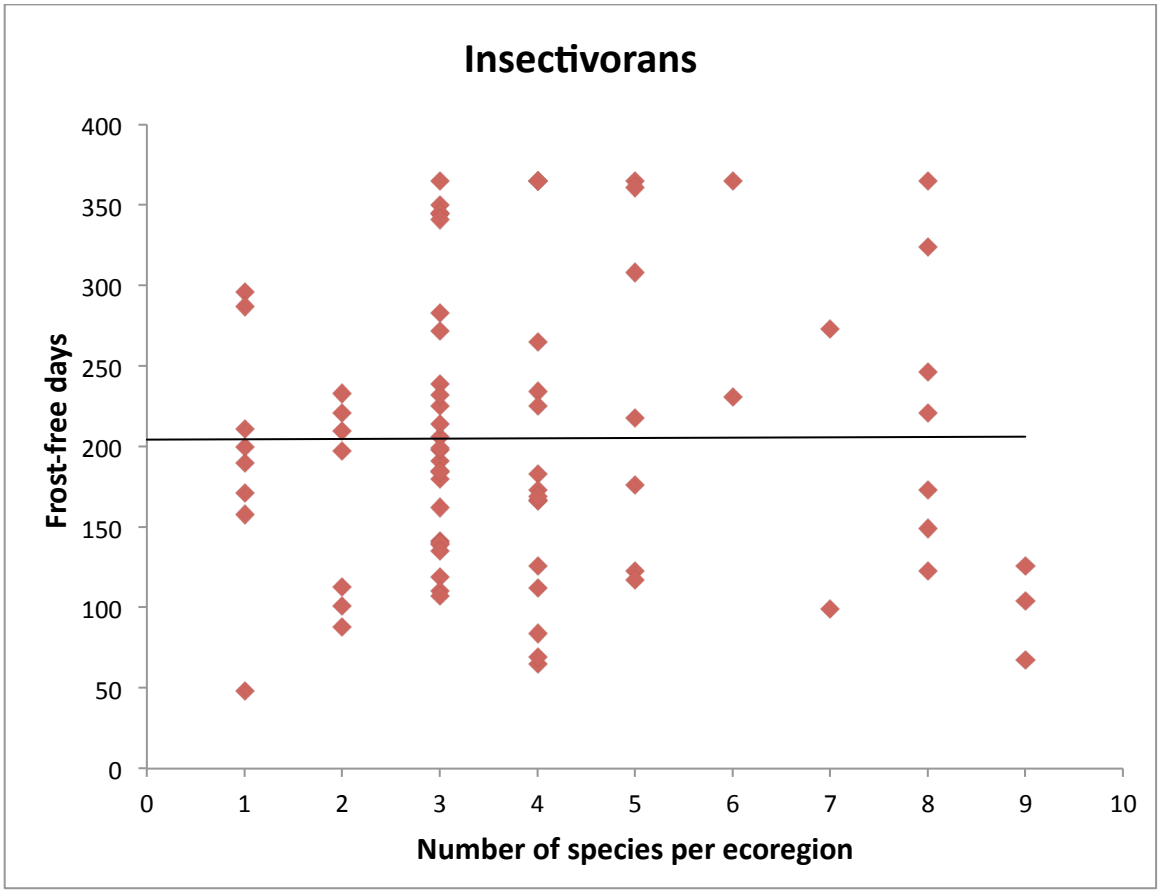


Figure 3.4. Plot of the number of species of insectivorans against the number of frost-free days per ecoregion.

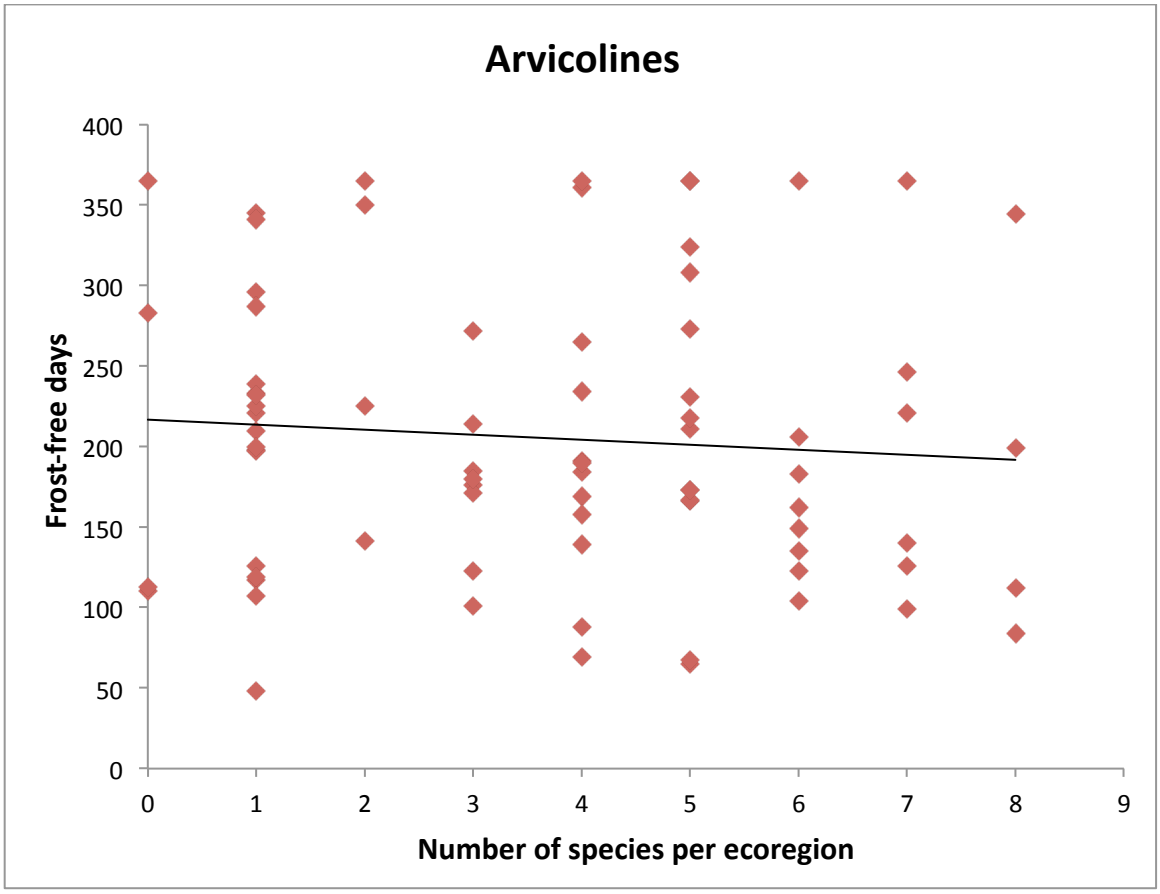


Figure 3.5. Plot of the number of species of arvicolines against the number of frost-free days per ecoregion.

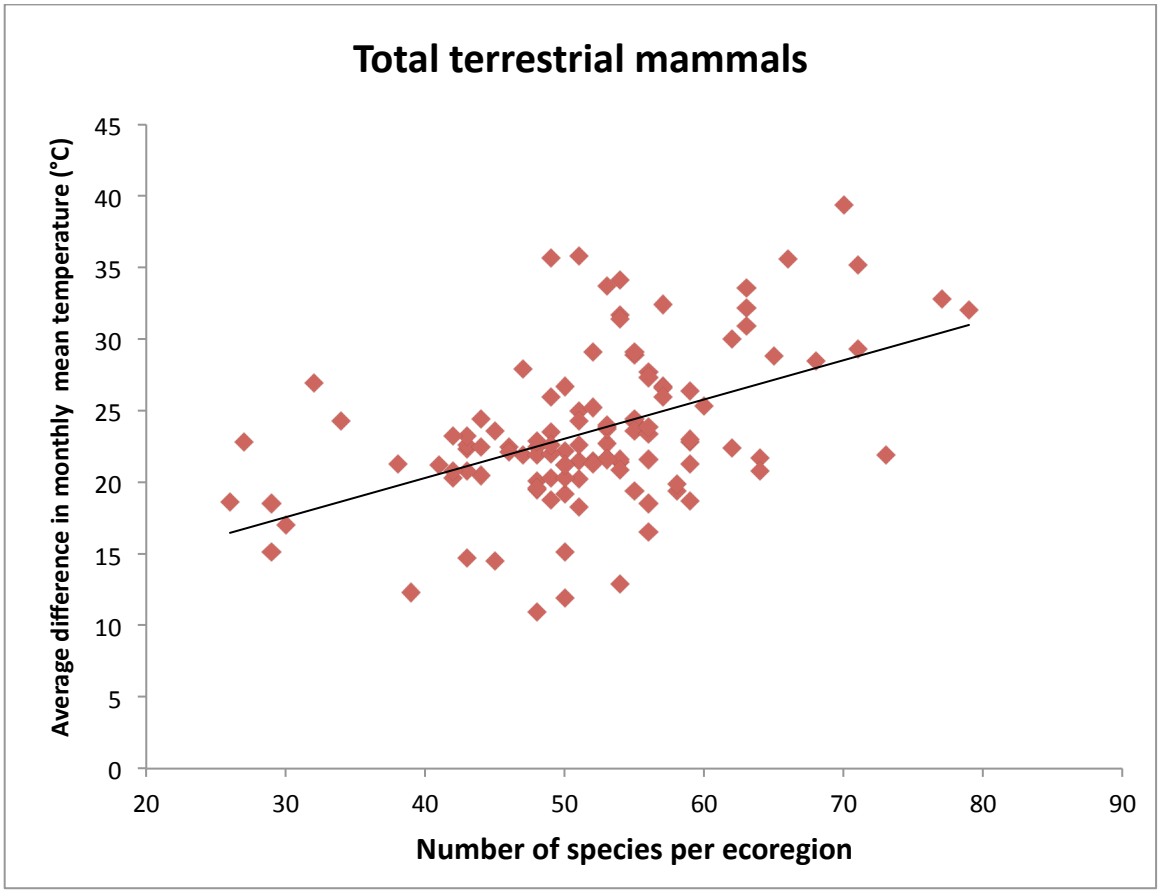


Figure 3.6. Plot of the number of species of total terrestrial mammals against the average difference in monthly mean temperature per ecoregion.

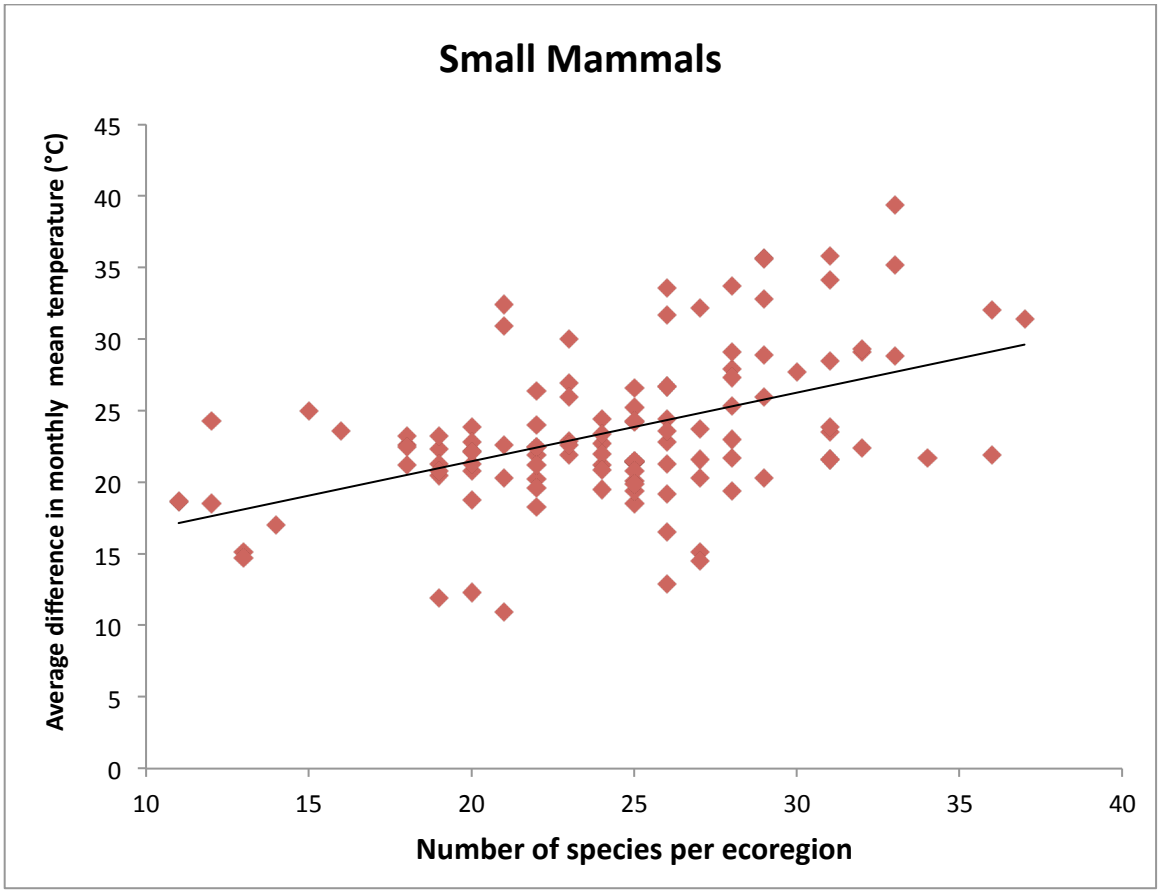


Figure 3.7. Plot of the number of species of small mammals against the average difference in monthly mean temperature per ecoregion.

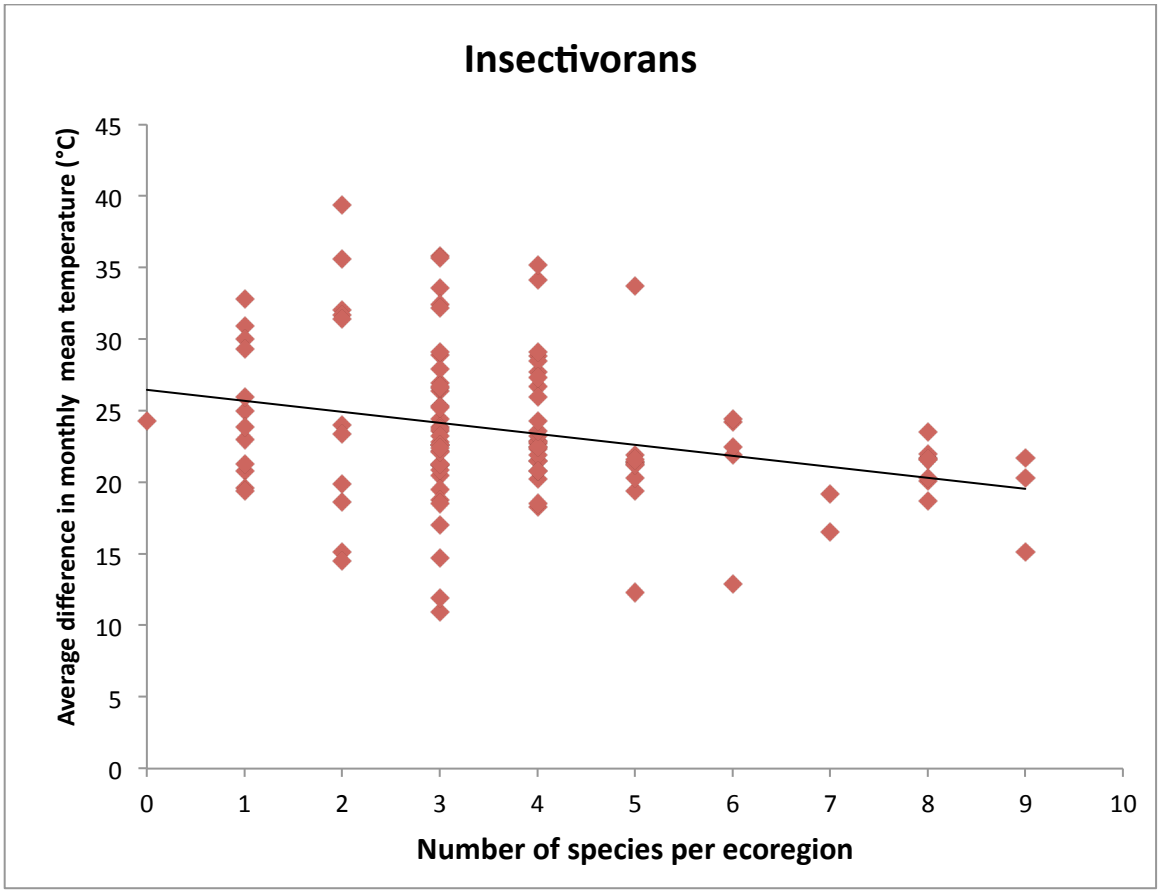


Figure 3.8. Plot of the number of species of insectivorans against the average difference in monthly mean temperature per ecoregion.

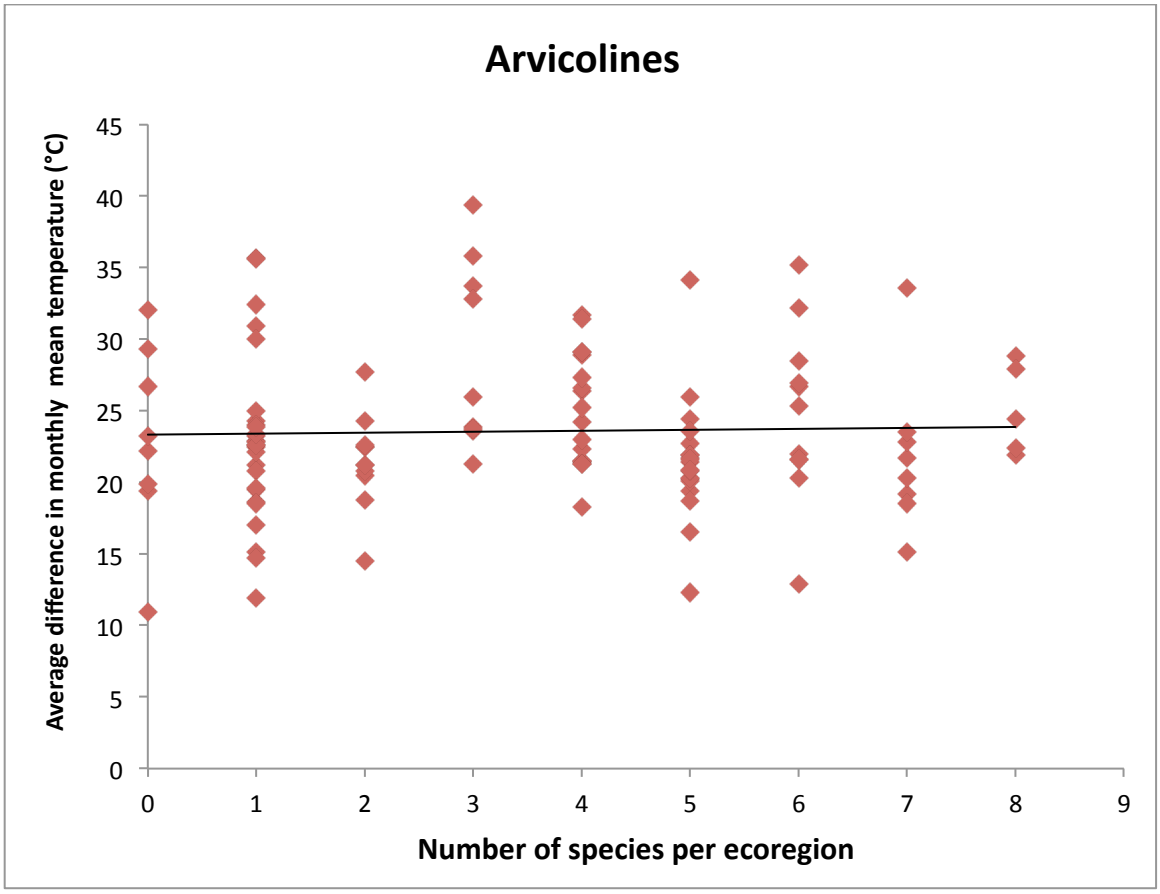


Figure 3.9. Plot of the number of species of arvicolines against the average difference in monthly mean temperature per ecoregion.

The plots of the maximum difference in mean monthly temperature to total mammals (Fig. 3.10), small mammals (Fig. 3.11), and arvicolines (Fig. 3.12) showed positive trends. Insectivorans (Fig. 3.13) showed a slightly negative trend to the maximum difference in mean monthly temperature. None of the correlations were significant.

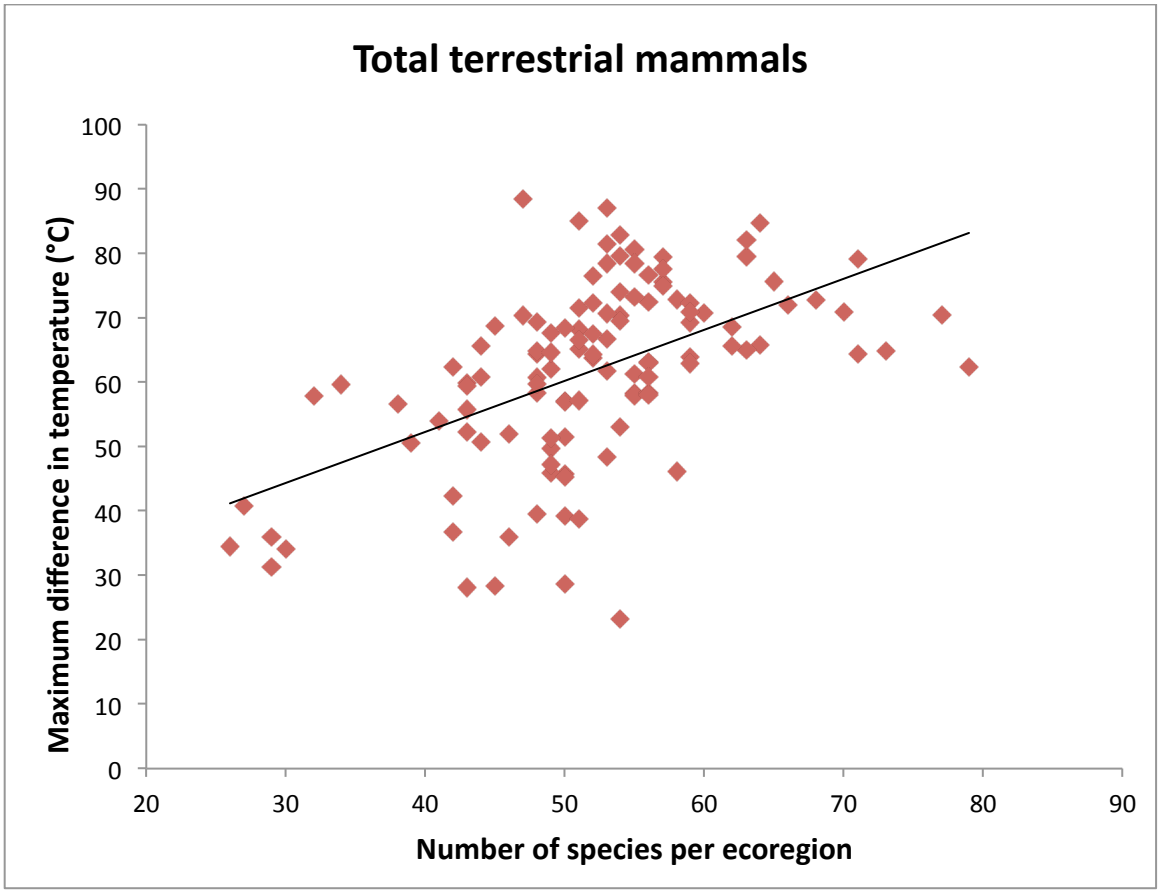


Figure 3.10. Plot of the number of species of total terrestrial mammals against the maximum difference in monthly mean temperature per ecoregion.

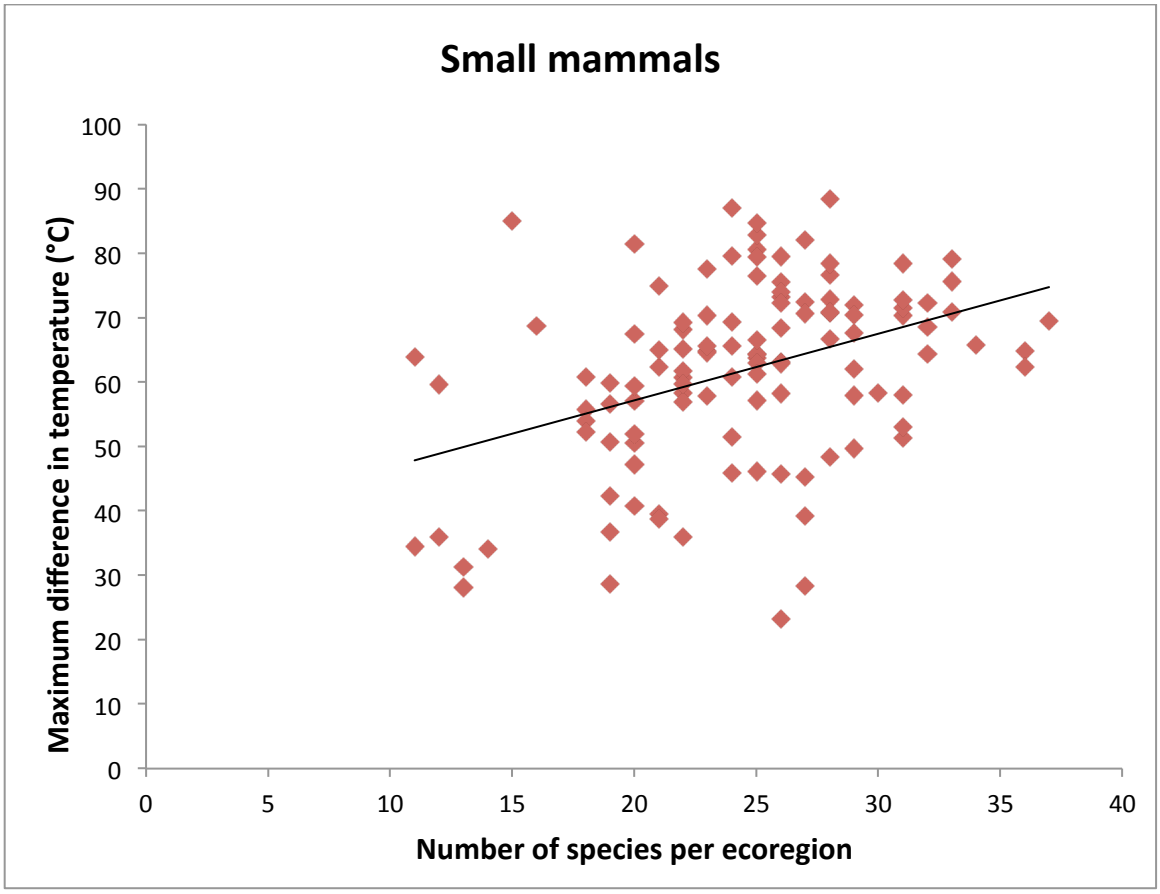


Figure 3.11. Plot of the number of species of small mammals against the maximum difference in monthly mean temperature per ecoregion.

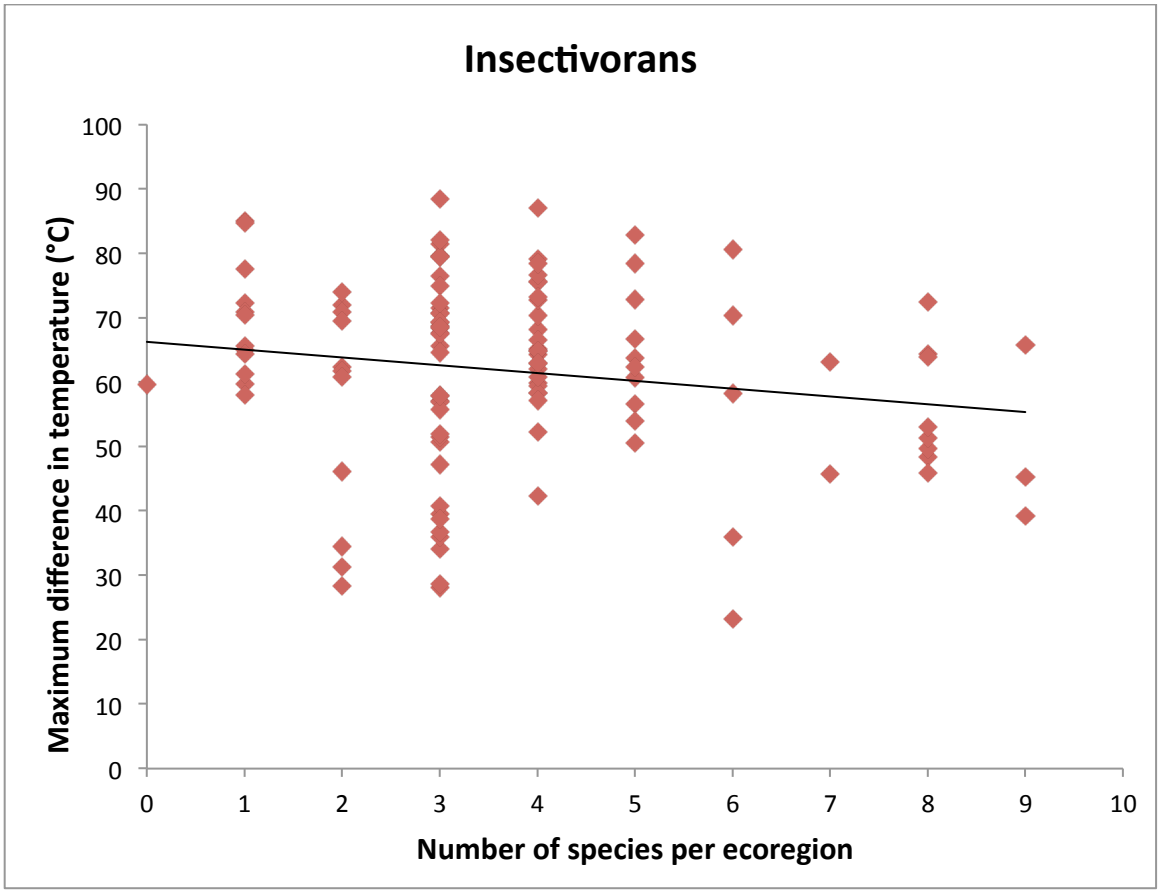


Figure 3.12. Plot of the number of species of insectivorans against the maximum difference in monthly mean temperature per ecoregion.

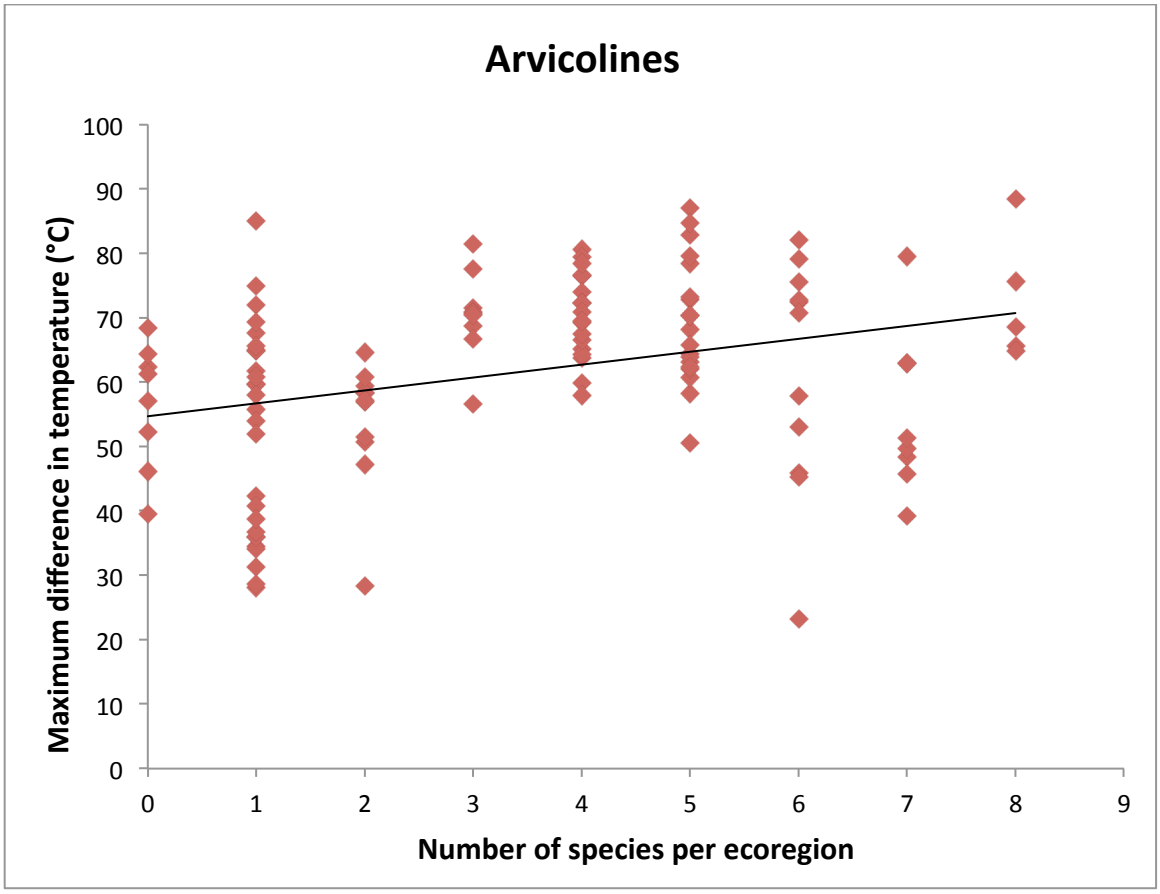


Figure 3.13. Plot of the number of species of arvicolines against the maximum difference in monthly mean temperature per ecoregion.

The total mammals (Fig. 3.14), small mammals (Fig. 3.15), and arvicolines (Fig. 3.16) showed a positive trend with the maximum difference in mean monthly high temperature, but none were significant. The insectivorans had essential zero correlation to the maximum difference in mean monthly high temperature (Fig. 3.17).

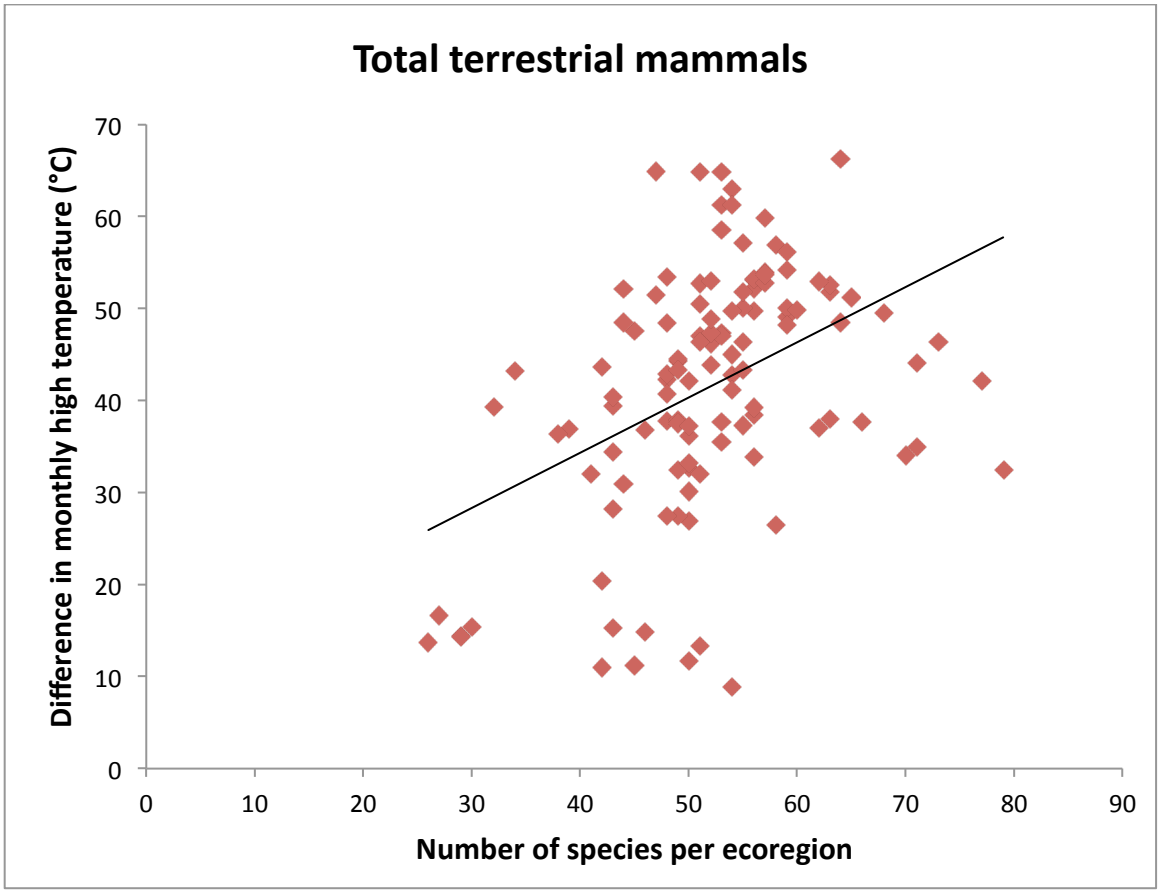


Figure 3.14. Plot of the number of species of total terrestrial mammals against the maximum difference in mean monthly high temperature per ecoregion.

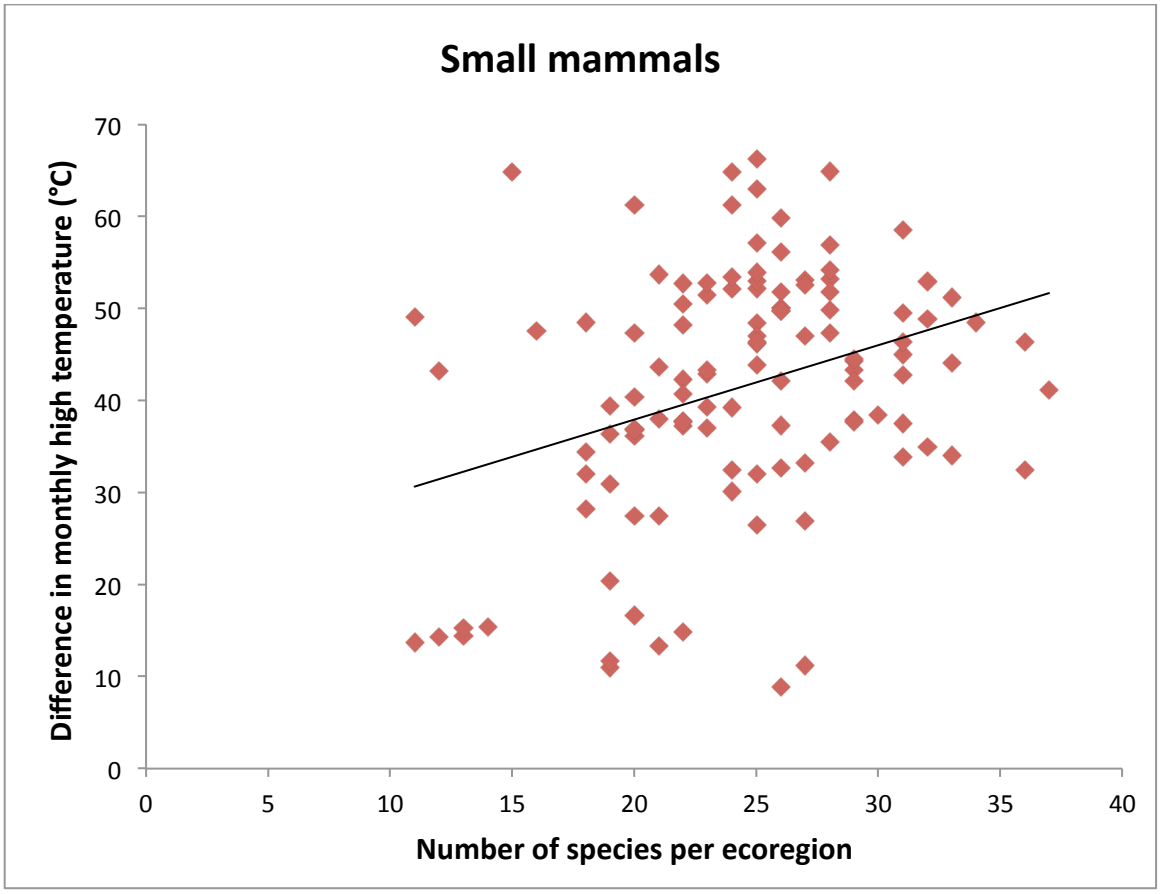


Figure 3.15. Plot of the number of species of small mammals against the maximum difference in mean monthly high temperature per ecoregion.

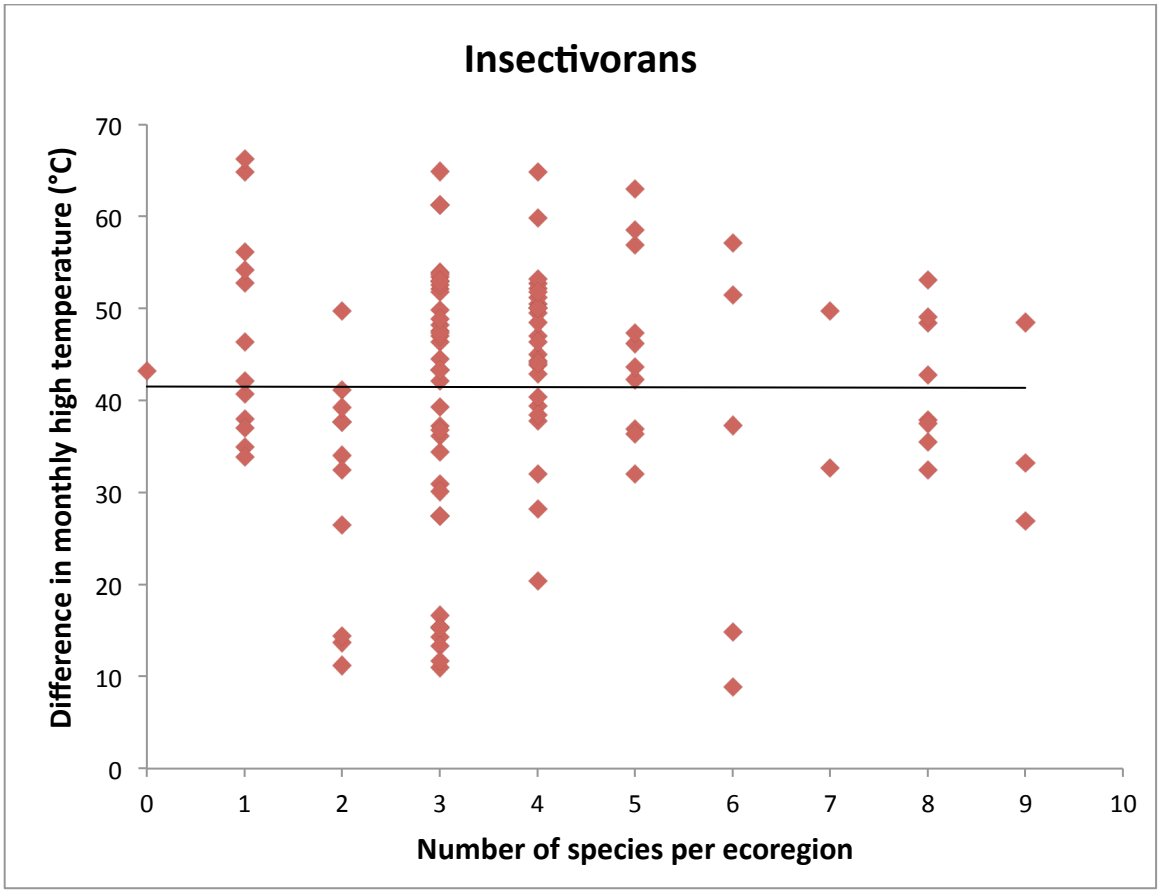


Figure 3.16. Plot of the number of species of insectivorans against the maximum difference in mean monthly high temperature per ecoregion.

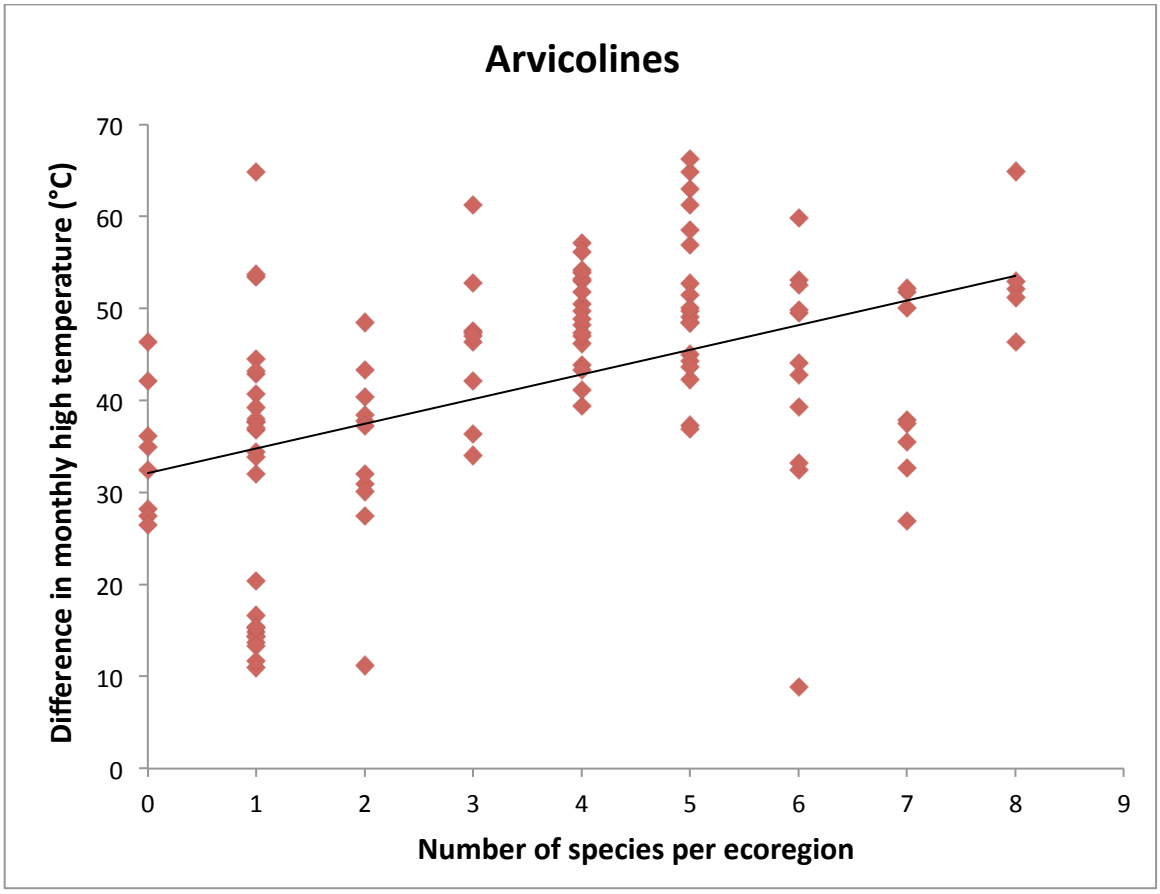


Figure 3.17. Plot of the number of species of arvicolines against the maximum difference in mean monthly high temperature per ecoregion.

The species-richness models I developed did not have any significant correlations. This was an unexpected result given that I hypothesized that the number of species of mammals would be more sensitive these climatic factors. I only used previously published species-richness models for my analysis of Hall's Cave. I first tested the ability of species-richness models to accurately reconstruct the present-day mean annual temperature near Hall's Cave (Fig. 3.18) using the sigmodontine (sensu Wilson and Reeder, 1993) mean

annual temperature models developed by Legendre et al. (2005) and Ruez (2007). Those models are based on modern species correlations so they should be able to accurately reconstruct present-day climatic conditions. There are 11 species of sigmodontines found in Kerr County today (Schmidly, 2004). The county is a much smaller geographic region than most used in either of the models, and within a single ecoregion (Griffith et al., 2007). Therefore, this test should be a conservative estimate of the number of species. The models yield an average annual temperature of 22.37 °C (Ruez model) and 23.0 °C (Legendre model). The average annual temperature for Junction, TX (nearest weather station to Hall's Cave) is 18.06 °C (National Climatic Data Center, 2002). The models generated temperatures 4.31 °C (23.9%) and 4.94 °C (27.3%) greater respectively.

A comparison of the models developed by Legendre et al. (2005) and Ruez (2007) showed similar trends for much of the Halls Cave sequence (Fig. 3.18). This is to be expected because they are both based on a linear equation with a single variable, the number of species of sigmodontines, and the values of the slopes and intercepts in both equations are similar. However, for the sequence above 245 cm (the depth at which the models begin giving temperatures of 0.6 °C or less) the average difference between the models is 27.8 percent.

The curves are based on a conservative or minimum number of species. Specimens assigned to *Reithrodontomys*, *Peromyscus*, or *Neotoma* were not identified to species (Toomey, 1993). Those genera are essentially impossible to identify to the species level based on skeletal material alone, but they contribute most of the species of sigmodontines found near the cave today. Historically, there are two species of *Reithrodontomys*, four species of *Peromyscus*, and three species of *Neotoma* from Kerr County (Schmidly, 2004). I only counted each of these genera as a single species for the Hall's Cave deposit. However, I also tested the effect of having recognized a larger

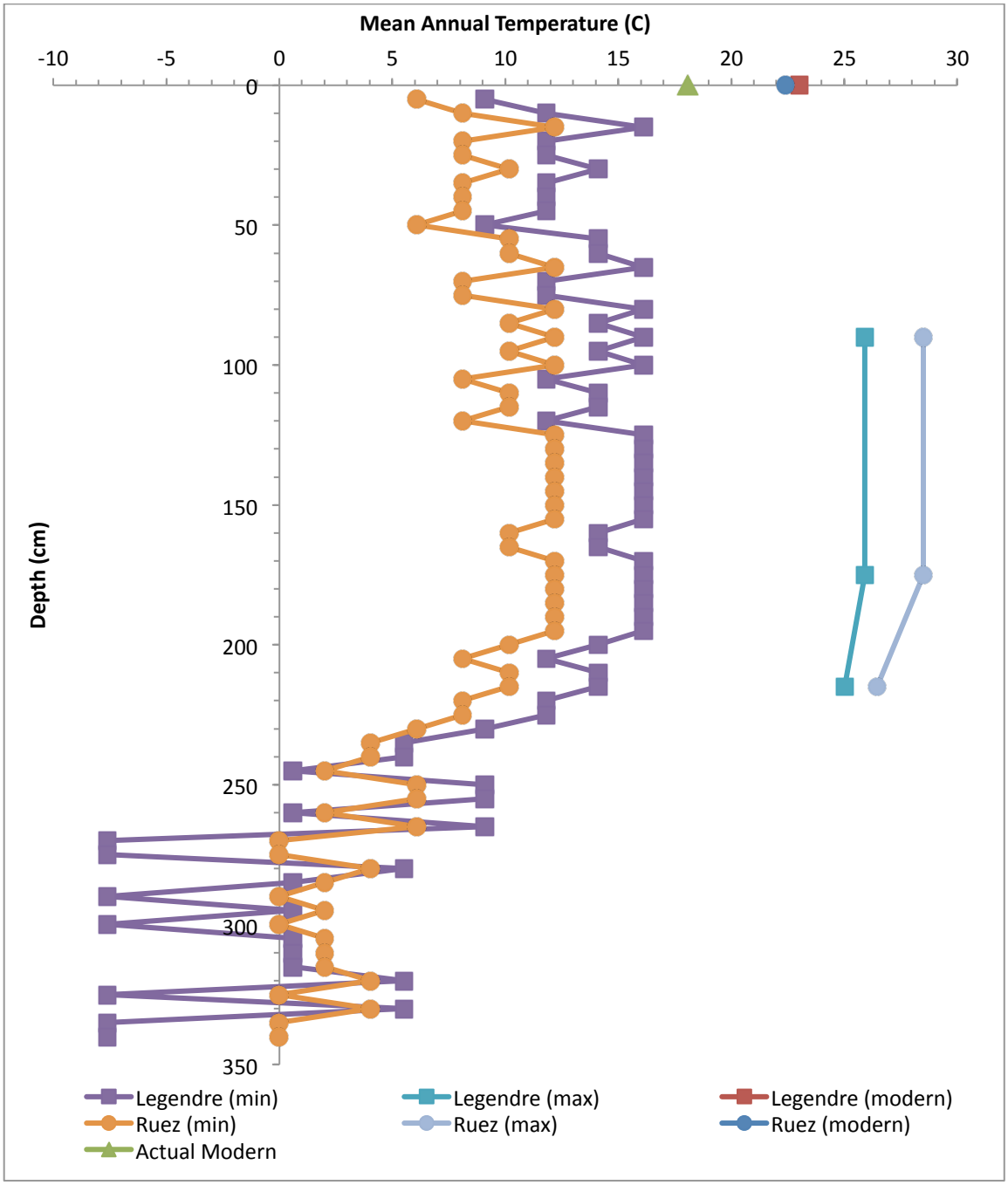


Figure 3.18. Various estimates of annual temperature based on species-richness models for sigmodontines (Legendre et al., 2005; Ruez, 2007).

number of species. I plotted the temperatures if all nine total species of *Reithrodontomys*, *Peromyscus*, and *Neotoma* were present from three arbitrary levels of Hall's cave, 85 cm, 170 cm, and 255 cm depths of the deposit (Fig. 3.18). Those depths represent roughly middle Holocene (85 cm), end of the Pleistocene (170 cm), and last glacial maximum (255 cm). The average annual temperature based on a single species of *Reithrodontomys*, *Peromyscus*, and *Neotoma*, and the other sigmodontines for 85 cm and 170 cm was 16.1 °C in the model developed by Legendre et al. (2005) and 14.1 °C in the model developed by Ruez (2007). The temperature increased to 25.9 °C and 28.5 °C in the respective models when all nine species were included. For 255 cm, the temperature increase was from 9.1 to 25.0 °C and from 6.1 to 26.4 °C in each model, respectively. This is an extreme range in potential temperature. The differences in temperature between the conservative estimate of species of sigmodontines and the high estimate of species roughly correspond to the difference between the annual temperatures of northern United States and the tropics (National Climatic Data Center, 2002). These data show that the models are extremely sensitive to the number of species that are identified.

I then tested several models developed by Ruez (2007) for various groups of mammals to determine if they could provide consistent reconstructions of past annual precipitation and mean annual temperature at Hall's Cave. Sigmodontinae had the highest correlation to mean annual temperature for the modern data, followed by Chiroptera, Arvicolinae, total-mammals, and small-mammals, and all correlations were significant to an alpha level of at least 0.001 (Ruez, 2007). The plots of temperatures generated for the excavation levels of Hall's Cave show conflicting signals between groups (Fig. 3.19). Chiroptera, Arvicolinae, and total-mammals show an increase in temperature from the bottom of the section to about 190 cm depth and then temperature decreases towards the top of the section. The sigmodontines also show an increase in temperature

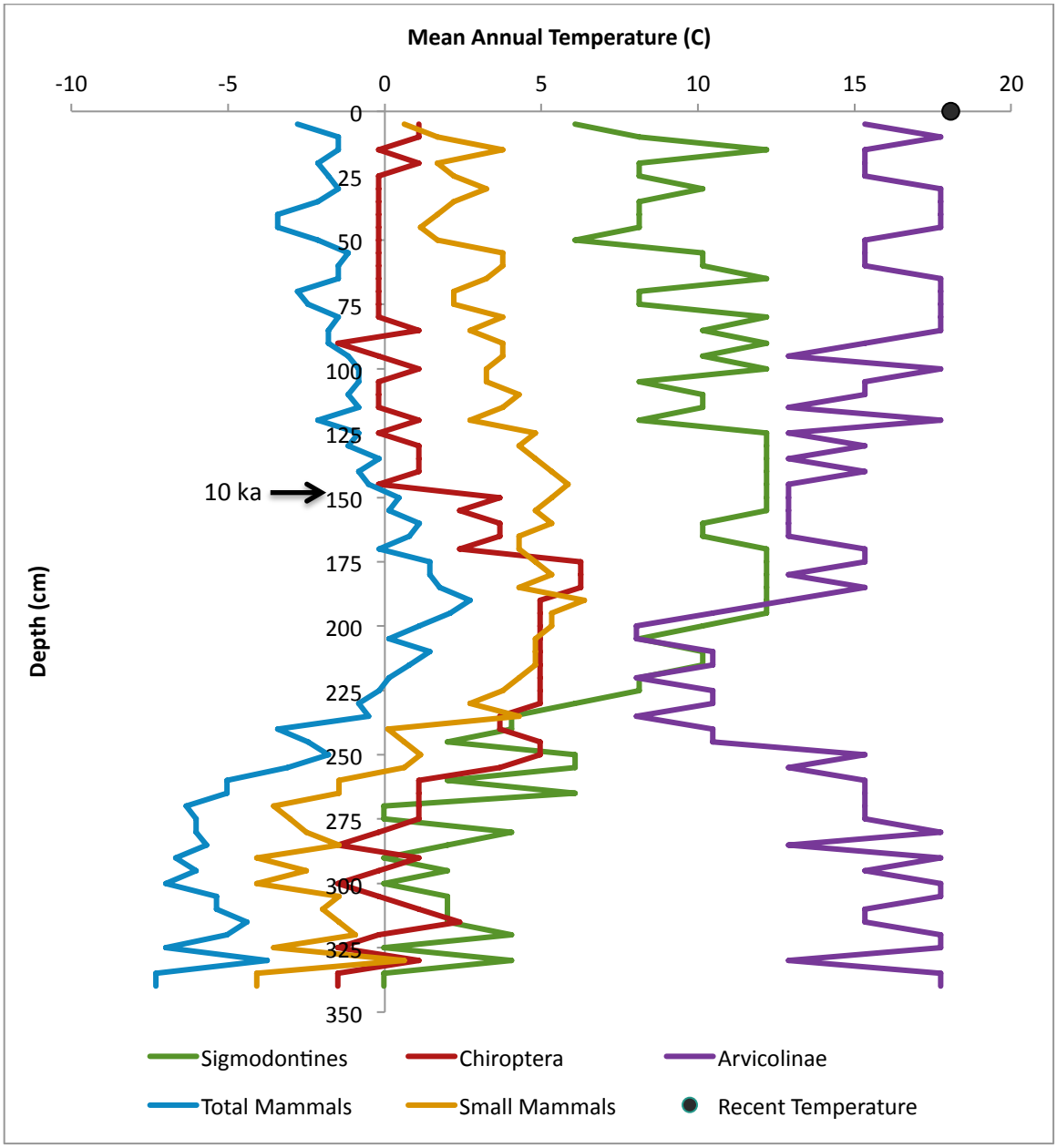


Figure 3.19 Estimated mean annual temperature derived from species-richness models developed by Ruez (2007) for the Hall's Cave sequence.

in the lower half of the section, but then remain somewhat constant in the upper half. The arvicolines show rapid oscillations in temperature from the bottom to about 250 cm depth, then a decrease to 200 cm, and then an increase in temperature to about the same as the lower part of the section.

The sigmodontines and arvicolines show opposite trends. However, the species diversity of both groups is strongly correlated with temperature in the modern North American biota. Arvicoline species diversity was the first model used to reconstruct past temperature (Montuire et al., 1997). These models are inconsistent with each other and there is no way to know which, if either, is a reliable indicator of past temperature.

The models developed by Ruez (2007) for the relationship between the number of species of mammals and average annual precipitation were less well correlated with the modern mammal biota than temperature. The insectivorans had the best correlation to the modern, and Artiodactyla and large-mammals (sensu Ruez, 2007) had correlations significant to an alpha level of at least 0.001. The rodents and arvicolines were significant to an alpha level of at least 0.01.

The precipitation data yielded conflicting results similar to those of the temperature models (Fig. 3.20). The insectivorans show an opposite trend to most of the other groups, and indicate about half as much precipitation as the other models. Both the rodent and arvicoline modes show similar trends, but only have similar absolute values below 170 cm. The Artiodactyla and the large-mammal precipitation data are similar to each other, but the large mammal data indicate more precipitation than the Artiodactyla model data. Both artiodactyls and arvicolines make up part of the large-mammal and rodent groups respectively, so the similar trends were expected. The absolute values of the precipitation derived from rodents, arvicolines, artiodactyls, and large-mammals are much wetter throughout the Holocene than modern precipitation, and do not show an

increase in precipitation in the Pleistocene. Like the temperature models, these models give inconsistent results.

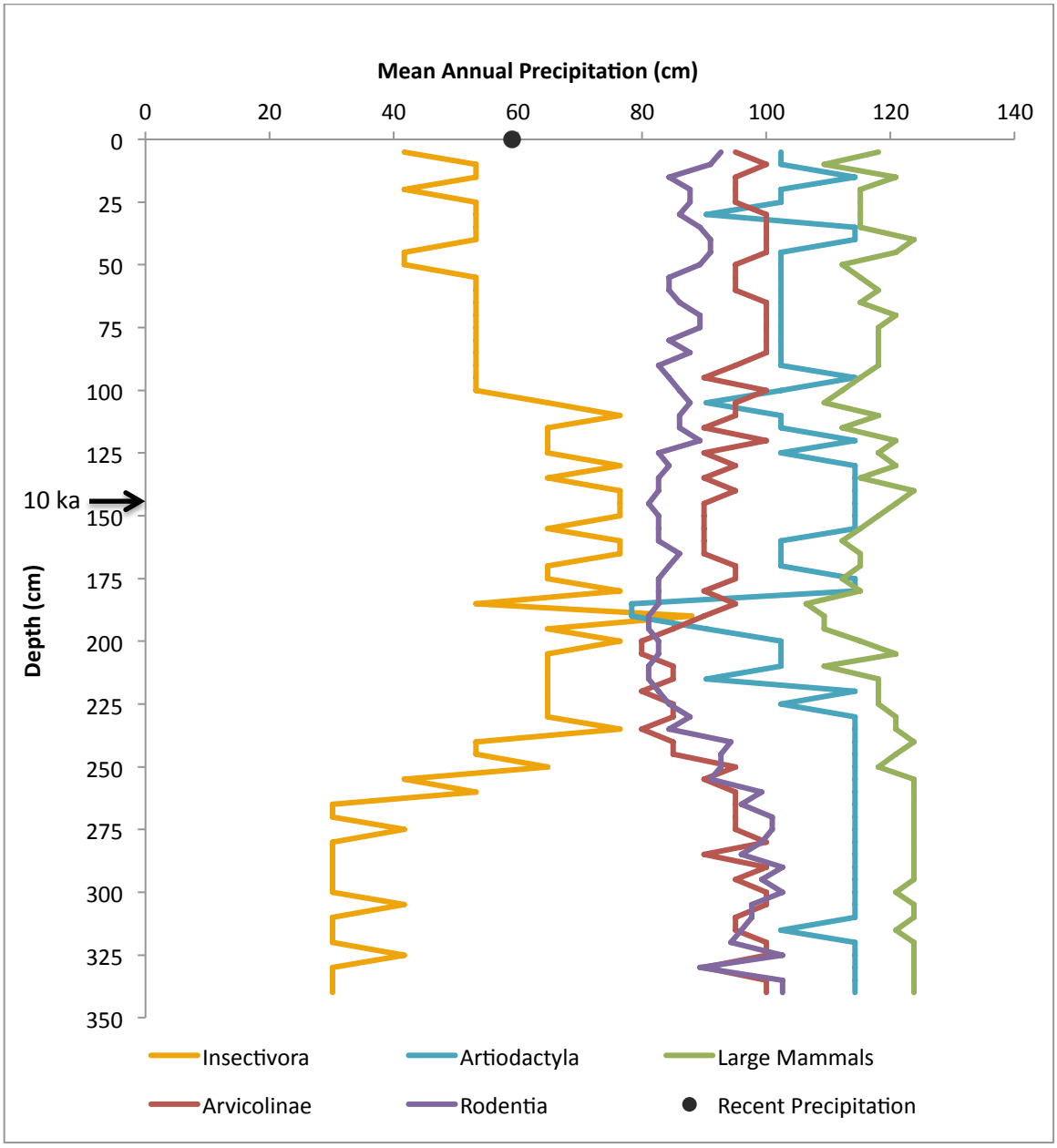


Figure 3.20. Estimated annual precipitation derived from species-richness models developed by Ruez (2007) for the Hall's Cave sequence.

Cenograms

My interpretation of the cenogram for the modern environment near Hall's Cave is that it has no change in slope in large or small mammals, and no gap in the medium-sized mammals (Fig. 3.21). Based on the methods proposed by Travouillon and Legendre (2009), that cenogram should indicate a humid, warm environment with a closed canopy. This is nothing like the actual environment near the cave. The cave is situated in an ecoregion characterized by oak savanna, and is close to the transition between subhumid and subarid (Griffith et al., 2007). This is a relatively dry, open-canopy environment, essentially the opposite of the interpretation yielded by the cenogram.

The cenogram generated from the mammals of the 60-65 cm excavation level of Hall's Cave represents the fauna from the middle Holocene (approximately 5 ka). That cenogram differed from the cenogram of modern mammals in several ways (Fig. 3.22). The middle Holocene cenogram has a large gap between the largest mammal (*Odocoileus* sp.) and the rest of the mammals, and there is only one large mammal so a slope cannot be determined. A large gap between small and large mammals traditionally was taken to indicate an open canopy, but the gap in traditional interpretations should be within the medium sized mammals (between mammals of 8 and 0.5 kg). This gap is between mammals with mass 55 kg (*Odocoileus* sp.) and 2.4 kg (*Lepus californicus*). There are four species (numbers 2-5 on the x-axis of Fig. 3.22) that mass between 8 and 0.5 kg. There is another gap between number 5 (0.81 kg) and 6 (0.22 kg). It is not clear from published interpretations (Legendre, 1986; Travouillon and Legendre, 2009) which gap should be interpreted to indicate an open canopy, so either gap could be interpreted as a mammal community from an open canopy, or if those are not the 'proper' gap then this would be interpreted as a closed community. The small mammals do not seem to have a steep slope that traditionally would be interpreted to indicate a cold environment. The slope is

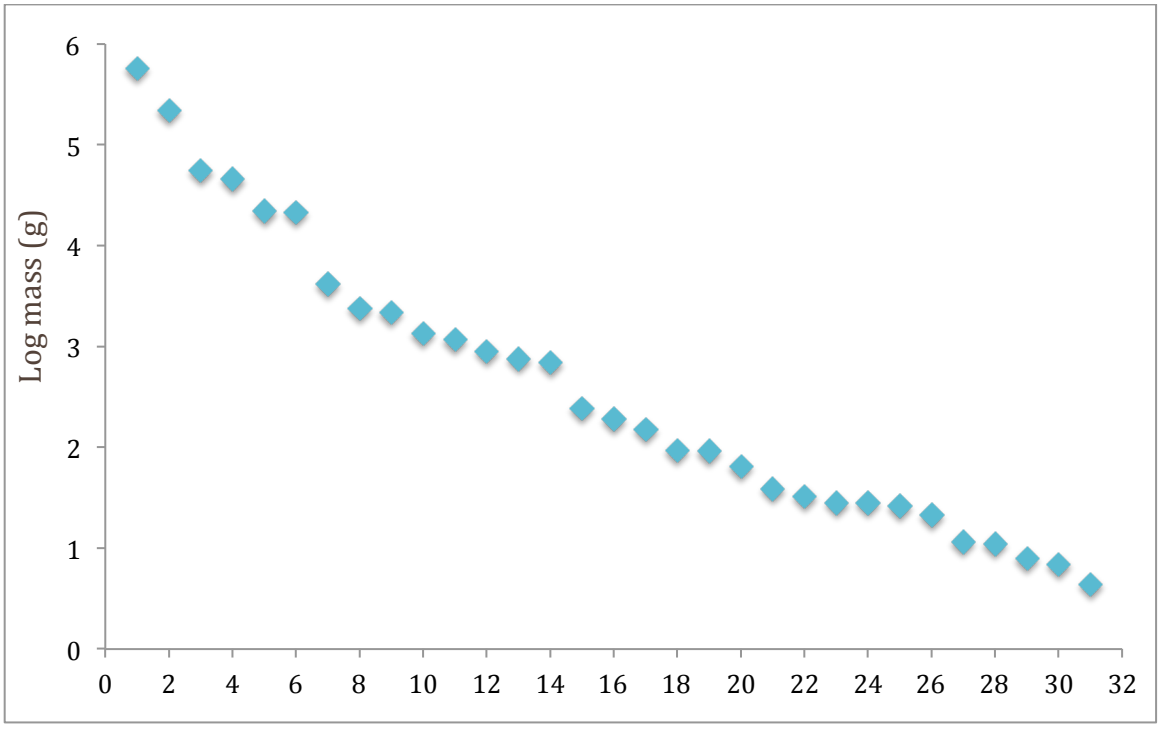


Figure 3.21. Cenogram of recent mammals from Kerr County, Texas. The x-axis is an ordered list of the mammals plotted in size from the largest (1) to the smallest (31).

possibly lower than the cenogram of recent mammals, but either interpretation would be possible. There is no way to control for relative slope if cenograms are not quantified.

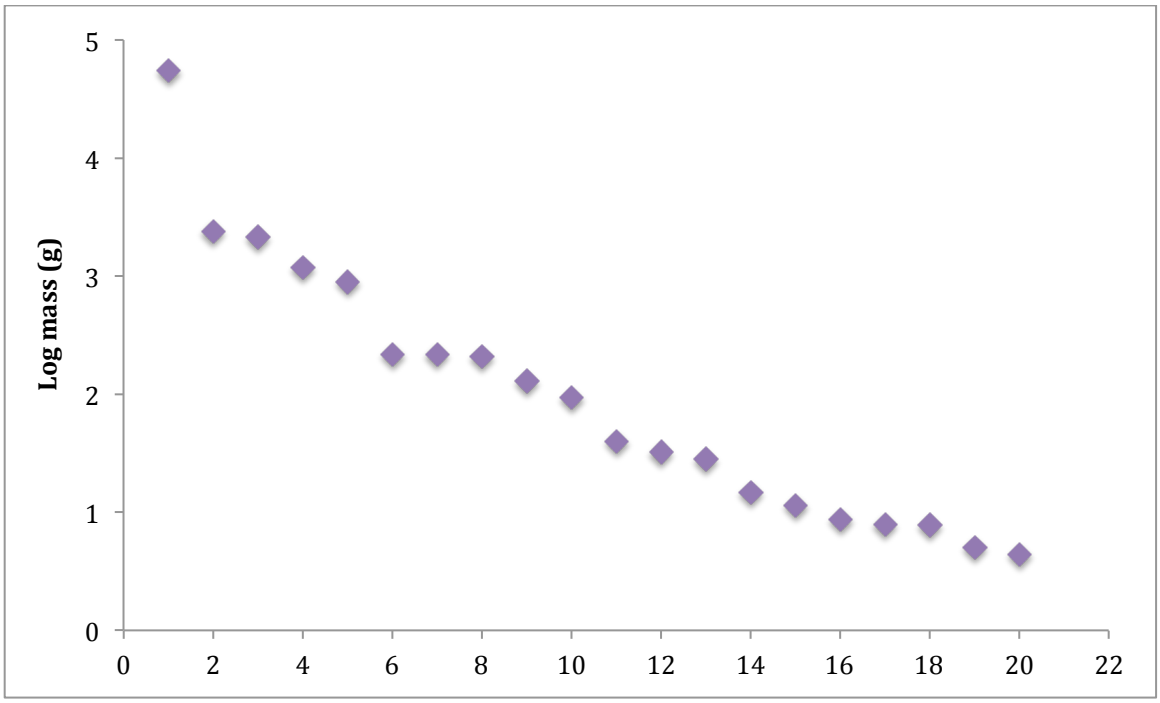


Figure 3.22. Cenogram plotted from level 60-65 cm of Hall's Cave. This interval represents the Middle Holocene. The x-axis is an ordered list of the mammals plotted in size from the largest (1) to the smallest (20).

The cenogram generated from the mammals of the 120-125 cm excavation level of Hall's Cave (Fig. 3.23) represents the fauna from the Pleistocene/Holocene transition (approximately 10 ka). That cenogram is almost identical to the middle Holocene cenogram. The Pleistocene/Holocene transition cenogram also has a significant gap between *Odocoileus* sp. and *Lepus californicus*, and another small one between taxa 5 and 6. Therefore, under traditional interpretations of cenograms, the reconstructed paleoenvironment of the terminal Pleistocene would be the same as that of the middle Holocene.

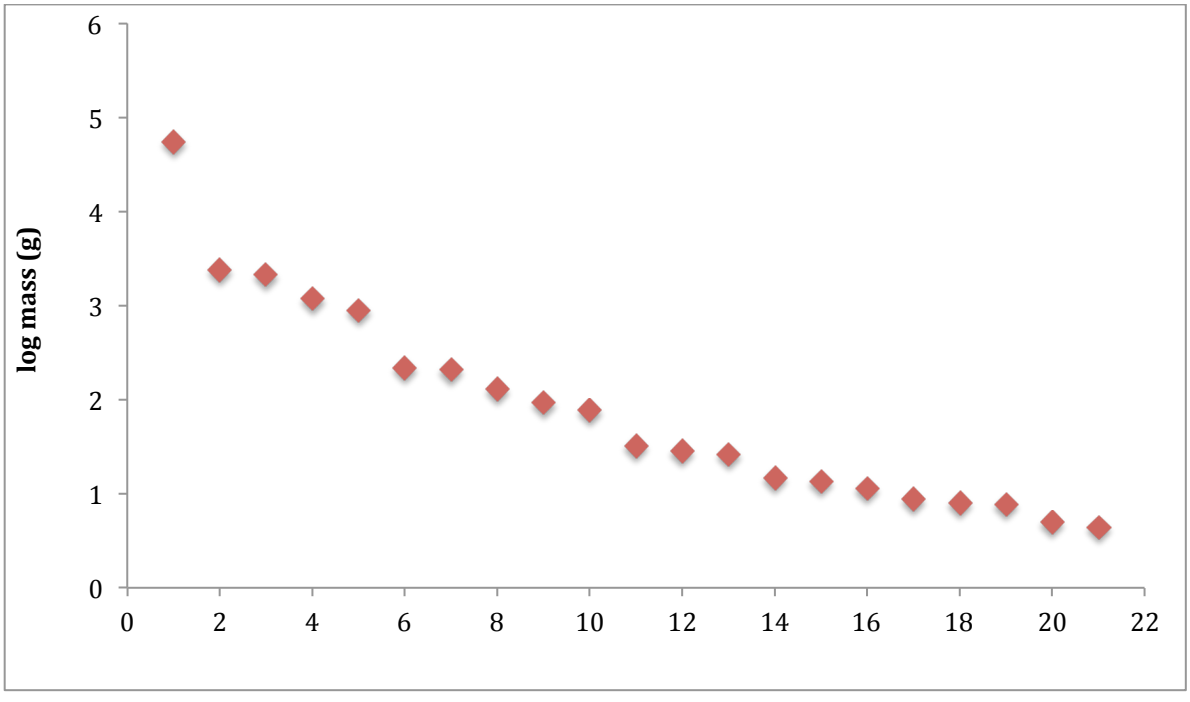


Figure 3.23. Cenogram plotted from level 120-125 cm of Hall's Cave. This interval represents the Pleistocene/Holocene transition. The x-axis is an ordered list of the mammals plotted in size from the largest (1) to the smallest (21).

The third cenogram I generated from Hall's cave comes from excavation layer 145-150 cm, and represents the latest Pleistocene (approximately 12 ka). The latest Pleistocene cenogram has no large mammals, so the plot is relatively flat (Fig. 3.24). Like the previous two cenograms, there appears to be a small gap between the 0.81 kg (number 4) and 0.22 kg (number 5) mammals. The large mammals are missing from this level, and this may indicate a preservational bias because they are present in layers above and below.

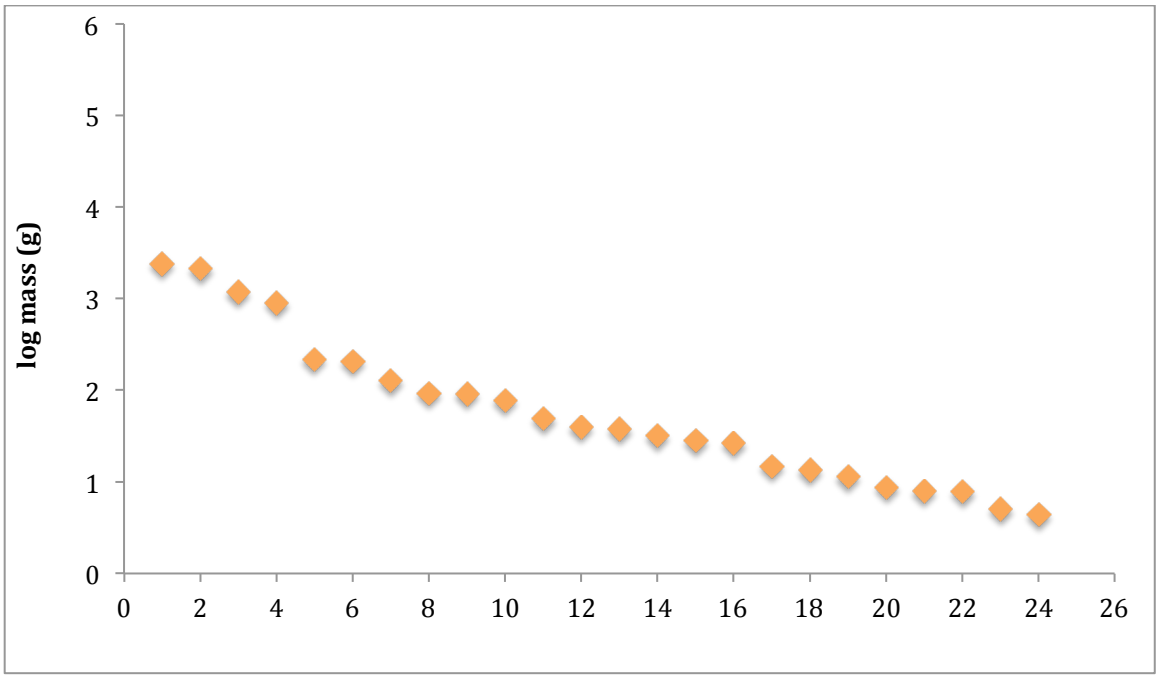


Figure 3.24. Cenogram plotted from level 145-150 cm of Hall's Cave. This interval represents the latest Pleistocene. Note there are no large (>8 kg) mammals from this level. The x-axis is an ordered list of the mammals plotted in size from the largest (1) to the smallest (24).

The final cenogram I generated was from 210-215 cm. That layer represents the late Pleistocene (approximately 15 ka) at Hall's Cave (Fig. 3.25). I included this interval because it represents the last glacial maximum, so the reconstructed environment should be the most different from today. Of the four cenograms from Hall's Cave, this is the only one to have enough large mammals to make an interpretation about aridity. I indicated my interpretations of the slope of the large and small mammals on this cenogram (Fig. 3.25). The large mammals seem to have a steeper slope, potentially indicating an arid environment. However, the first part of the small mammal portion of the cenogram has a similar slope, but I drew the line through all of the small mammals. Without any quantification, any interpretation of slope could be valid, and therefore, there is no rigor to the paleoenvironmental interpretations.

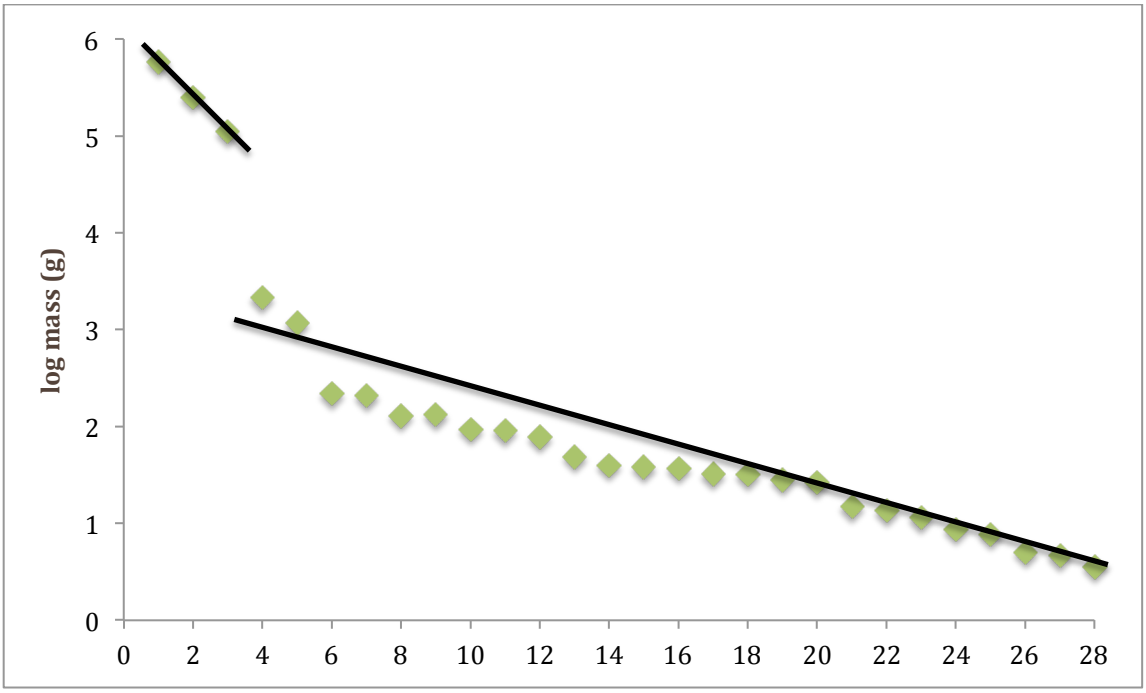


Figure 3.25. Cenogram plotted from level 210-215 cm of Hall's Cave. This interval represents the late Pleistocene. This level has three large mammals. One possible interpretation of the slope of the large and small mammals is shown. The x-axis is an ordered list of the mammals plotted in size from the largest (1) to the smallest (28).

DISCUSSION

Problems with species-richness models

1. Higher-order taxonomy

The first problem with species-richness models is that higher-order taxonomy of mammals is not fixed, but the species-richness models are tied to specific taxonomic or ecological groups. The sigmodontine model developed by Legendre et al. (2005) used a now out-of-date taxonomy. Sigmodontine rodents are members of the subfamily Sigmodontinae. The taxonomy used by Legendre et al., (2005) was based on Wilson and Reeder (1993). Ruez used the taxonomy of the updated checklist of North American mammals (Baker, Bradley, et al., 2003). That checklist does not include subfamilies, but based on the numbers of species of sigmodontines in the analysis the model likely included the species classified as Sigmodontinae by Wilson and Reeder (1993).

Sigmodontinae as used by Wilson and Reeder (1993) included most of the rats and mice native to North and South America, such as *Peromyscus*, *Neotoma*, *Reithrodontomys*, and *Sigmodon*. Later work restricted the number of taxa included in Sigmodontinae so that the only North American taxa are *Sigmodon* and *Oryzomys* (Wilson and Reeder, 2005). The other genera were transferred to the subfamily Neotominae. The species richness correlations are entirely based on the number of species. If a subsequent analysis used the most recent taxonomy then most of the species of North American sigmodontines would not included. This would have a profound impact on environmental reconstructions. Though not stated in any of the species-richness papers, taxonomic practice has a significant impact on the analyses. The taxonomy of many groups of mammals is regularly revised with new data and analyses (Wilson and Reeder, 2005). Therefore, this could be an additional source of error in these

models. It is doubtful that their results would have been the same if Legendre et al. (2005) used the most recent taxonomy. If modern mammalian taxonomy is in flux then this problem is only exacerbated for extinct taxa. Not all species-richness models were developed for monophyletic taxa. Several models developed by Ruez (2007) used small or large mammals and had good correlations with the modern biota. These models are sensitive to species numbers, so which species are included in the group must be the same or else the analysis will never yield useful results.

2. Fossil Identification

The most significant problem applying species-richness models to fossil localities is that fossil identifications can have a profound impact on the number of species. The inability to differentiate closely related species would skew the results. This is especially significant for disarticulated small mammals because in most cases species resolution cannot be obtained (Bell and Bever, 2006; Chapter 2). This was acknowledged and discussed by Ruez (2007), but it was not acknowledged by earlier authors (Montuire et al., 1997; Legendre et al., 2005). The identification of small mammals from Quaternary sites is fraught with difficulties. Most of the material that is recovered and used for identification is isolated teeth and jaws. There are a limited number of morphological characters to use for identification, and though some species level identification is possible within select clades (Chapter 2), it is nearly impossible for most small mammals without using significant assumptions of the geographic and temporal range of fossils (Chapter 4). The traditional identification of shrews from North American Quaternary sites uses morphological characters to identify the genus, and then the geographic location of the fossil is used to apply the species epithet (Chapter 2). This procedure is

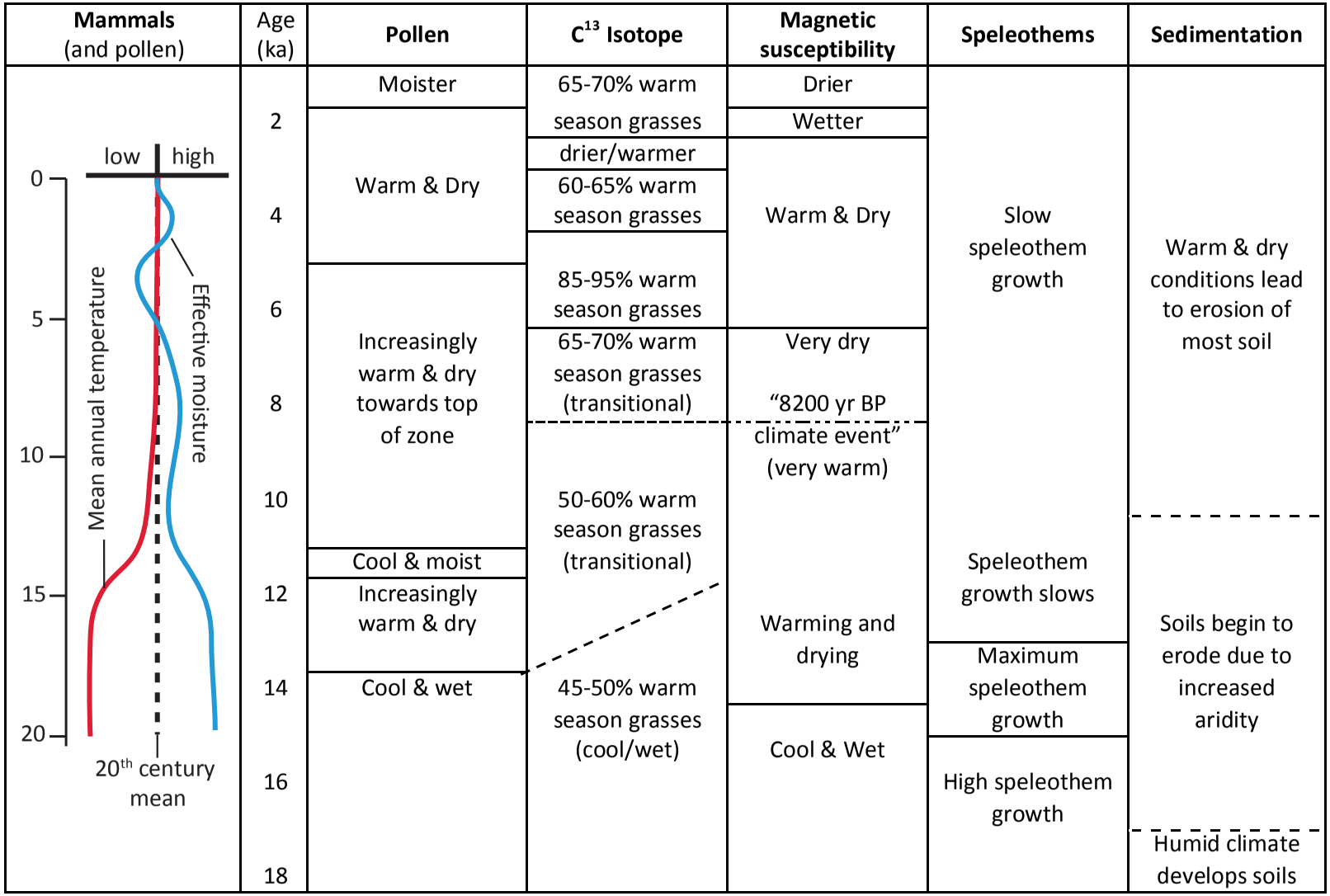
often used for other small mammals, or specimens are only identified to genus. Therefore, the number of identified species in the Quaternary fossil record is either inflated from the use of geographic assumptions to identify species, or underrepresented because it is not possible to differentiate species based solely on craniodental characters. That will prevent any accurate reconstruction of paleoenvironment from species-richness models.

Though cave deposits tend to sample accurately the local biota of small mammals (Hadly, 1999), this is not true of most paleontological deposits, making the wide application of this method for interpreting past environments extremely biased. Many factors can cause a preservation bias at a fossil locality. Taphonomic processes could selectively eliminate species. If these models do not work for a Holocene-to-Pleistocene assemblage in which the species are most similar to extant species, there is no reason to accept that they are applicable to any older faunas.

3. Incongruity with paleoenvironmental proxies

The general trend of paleoenvironment in central Texas from the latest Pleistocene to the present is warming and drying (Fig. 3.26). I treat central Texas as equivalent to the Edwards Plateau. There are a number of independent paleoenvironmental proxies from central Texas as shown in Figure 3.26. These are C^{13} isotopes of soil carbonates (Nordt et al., 1994), speleothem growth rates (Musgrove et al. 2001), soil erosion rates (Cooke, 2005), magnetic susceptibility of cave sediments (Ellwood and Gose, 2006), and pollen records (Boulter et al., 2010). The oldest paleoenvironmental records from central Texas are 18 to 14 ka. During that interval, it was much wetter and cooler on the Edwards Plateau. Around 12 ka a warming and

Figure 3.26. Summary of paleoenvironmental proxies for the Edwards Plateau. Pollen from Boulter et al., 2010; C13 isotopes, Nordt et al., 1994; magnetic susceptibility, Elwood and Gose, 2006; speleothems, Musgrove et al., 2001; sedimentology, Cooke, 2005. The mammals are a qualitative interpretation based primarily on the Hall's Cave fauna (Toomey et al., 1993)


Mammals (and pollen)
Age (ka)
Pollen
C13 Isotope
Magnetic susceptibility
Speleothems
Sedimentation
low
high
0
5
10
15
20
Mean annual temperature
Effective moisture
20th century mean
2
4
6
8
10
12
14
16
18
Moister
Warm & Dry
Increasingly warm & dry towards top of zone
Cool & moist
Increasingly warm & dry
Cool & wet
65-70% warm season grasses
drier/warmer
60-65% warm season grasses
85-95% warm season grasses
65-70% warm season grasses (transitional)
50-60% warm season grasses (transitional)
45-50% warm season grasses (cool/wet)
Drier
Wetter
Warm & Dry
Very dry
"8200 yr BP climate event" (very warm)
Warming and drying
Cool & Wet
Slow speleothem growth
Speleothem growth slows
Maximum speleothem growth
High speleothem growth
Warm & dry conditions lead to erosion of most soil
Soils begin to erode due to increased aridity
Humid climate develops soils

drying trend began and from 10 to 8 ka, temperature and precipitation were similar to today. The C^{13} isotopes, magnetic susceptibility, and pollen records are detailed enough to show that much of the Holocene was even drier than today, but with short wetter periods (Nordt et al., 1994; Ellwood and Gose, 2006; Boulter et al., 2010). These proxies indicate that the maximum dry conditions occurred around 5 ka. There was likely another cool, humid period around 2 ka. After 2 ka, climatic conditions were similar to today.

The species-richness models do not agree with the proxies shown in Figure 3.26. The absolute temperature values for Hall's Cave that were recovered by the various models are unrealistic, and inconsistent with all other proxies for temperature. None of the independent proxies yield specific temperature predictions, but is likely that conditions on the Edwards Plateau during the late Pleistocene and early Holocene were a few °C cooler than today (Nordt et al., 1994; Ellwood and Gose, 2006; Boulter et al., 2010). If the data derived from some of the species-richness models for some groups (e.g., sigmodontines [Fig. 3.18], total mammals, Chiroptera and small mammals [Fig. 3.19]) are accurate, it would indicate that the mean annual temperature was close to 0 °C or below for much of the Holocene and Pleistocene. This is much colder than the temperature suggested by the independent proxies.

Though there is little similarity in the relative changes in temperature between the species-richness models and the paleoenvironmental proxies, it was suggested this type of model would accurately estimate temperature (Montuire et al., 1997; Legendre et al., 2005). The temperatures reconstructed by these models are unexpectedly cold. It is unlikely that mean annual temperature in central Texas was ever below 0 °C even during the last glacial maximum, let alone throughout the Holocene. Other paleoenvironmental proxies are suggestive of cooler conditions, but do not indicate a mean annual

temperature as cold as the species-richness models (Nordt et al., 1994; Musgrove et al., 2001; Cooke, 2005; Ellwood and Gose, 2006; Boulter et al., 2010).

The extremely cold temperatures generated from the species-richness models do not reflect actual temperature, but instead represent the bias of the number of identified species. As shown in Figure 3.18, a change in the number of identified species will strongly affect the model. It is likely that the total number of species is underrepresented in individual layers at Hall's Cave. Hall's Cave was excavated in relatively thin (5 cm) excavation units, so the amount of time-averaging per layer is limited. This means that the total number of species per layer is relatively low compared to the number of species that could have been preserved. The species-richness models for temperature reflect a positive relationship between numbers of species and temperature: the higher the average annual temperature the more species of mammals. Therefore, the species-richness models do not record change in temperature through time, but merely the change in number of species preserved in each level of Hall's Cave. Yet, a species-richness model was used to provide exact temperature values for fossil localities in Europe from the Miocene through the Pleistocene (Montuire et al., 2006).

Even the trends of the data derived from species-richness models are not similar to the proxies. The data resulting from the Sigmodontinae, Chiroptera, total-mammals, and small-mammal models show a warming trend from the Pleistocene to the Holocene, but the maximum temperature generated by those models occurs before the end of the Pleistocene (Fig. 3.19). The data from the Chiroptera, total-mammals, and small-mammal models show a slight cooling through the Holocene to the present. The data from the Arvicolinae model indicate the coldest temperatures of about 15 to 12 ka. However, the temperature earlier in the Pleistocene is as warm as most of the Holocene. Those reconstructions are contradictory to all the independent proxies.

The precipitation values from the species-richness models also are not realistic when compared to the independent proxies. The precipitation models also are biased by the number of identified species. The absolute precipitation values are meaningless and contrary to the independent proxies. The data derived from the Insectivora model for the bottom quarter of the deposit indicate low precipitation, but are Pleistocene in age (Fig. 3.20). The independent proxies indicate that this should be the wettest interval (Fig. 3.26). Only the Insectivora model data have distinct differences through the deposit. However, the trend of the data could be caused by a preservation bias. The Hall's Cave sequence is much less fossiliferous in the lower part of the section, and there are no insectivorans in some of the lower levels. The low numbers could be caused because insectivorans were not preserved in the deposit or because they were missing from the area around Hall's Cave. The Insectivora model is sensitive enough to show that there are fewer species present in the lower part of the deposit. The other mammals have poorer correlations to modern precipitation; therefore, those models only show slight differences in precipitation when the number of species changes.

Problems with cenograms

1. No quantification of cenograms

It was suggested previously that cenograms cannot be quantified and therefore are not rigorous paleoenvironmental tools (Rodriquez, 1999). In response to that paper, it was suggested by Travouillon and Legendre (2006) that cenograms only be examined qualitatively. This creates a significant problem because there is no consistent way to scale them. To highlight how easy it is to manipulate the shape of a cenogram to produce any result, I compared two versions of the late Pleistocene (12 ka) cenogram from Hall's

Cave (Fig. 3.27) to the original cenogram shapes (cenograms A-F) of modern faunas developed by Legendre, (1986). Cenogram 1 (Fig. 3.27) appears to be most similar to cenogram A or B at the top of the figure. Cenogram A, was drawn by Legendre, (1986) for High Invindo, a tropical rainforest in Gabon and cenogram B, was drawn from Kagera Park, a tropical wooded savanna found in Rwanda. Cenogram 2 (Fig. 3.27) uses the exact same species from 12 ka at Hall's cave, but I changed the height and width of the plot. This cenogram closely resembles E, the cenogram drawn from the desert of Aghbolagh, Iran or F, the cenogram drawn from the Mediterranean arid zone of Doñana National Park, Spain. The latter would be most similar to the environment found near Hall's cave today, but it is probable that none of those is similar to the environment of central Texas in the Late Pleistocene.

2. Size bias in the fossil record

The latest Pleistocene cenogram from levels 145-150 cm (Fig. 3.24) is unlike any of the example modern cenograms published by Legendre (1986). The problem is that there are no large mammals in this stratigraphic level. This is a major issue with using cenograms to make interpretations about environments at the time of deposition of fossil deposits. There are many biases in the fossil record and body-size bias is one potential source of bias. For example, no proboscidians known from Hall's Cave, but a nearby cave, Friesenhahn Cave contained a large number of individuals (Graham, 1976). Size bias will have a significant impact on the interpretations of cenograms because cenograms are dependent on having the complete fauna represented.

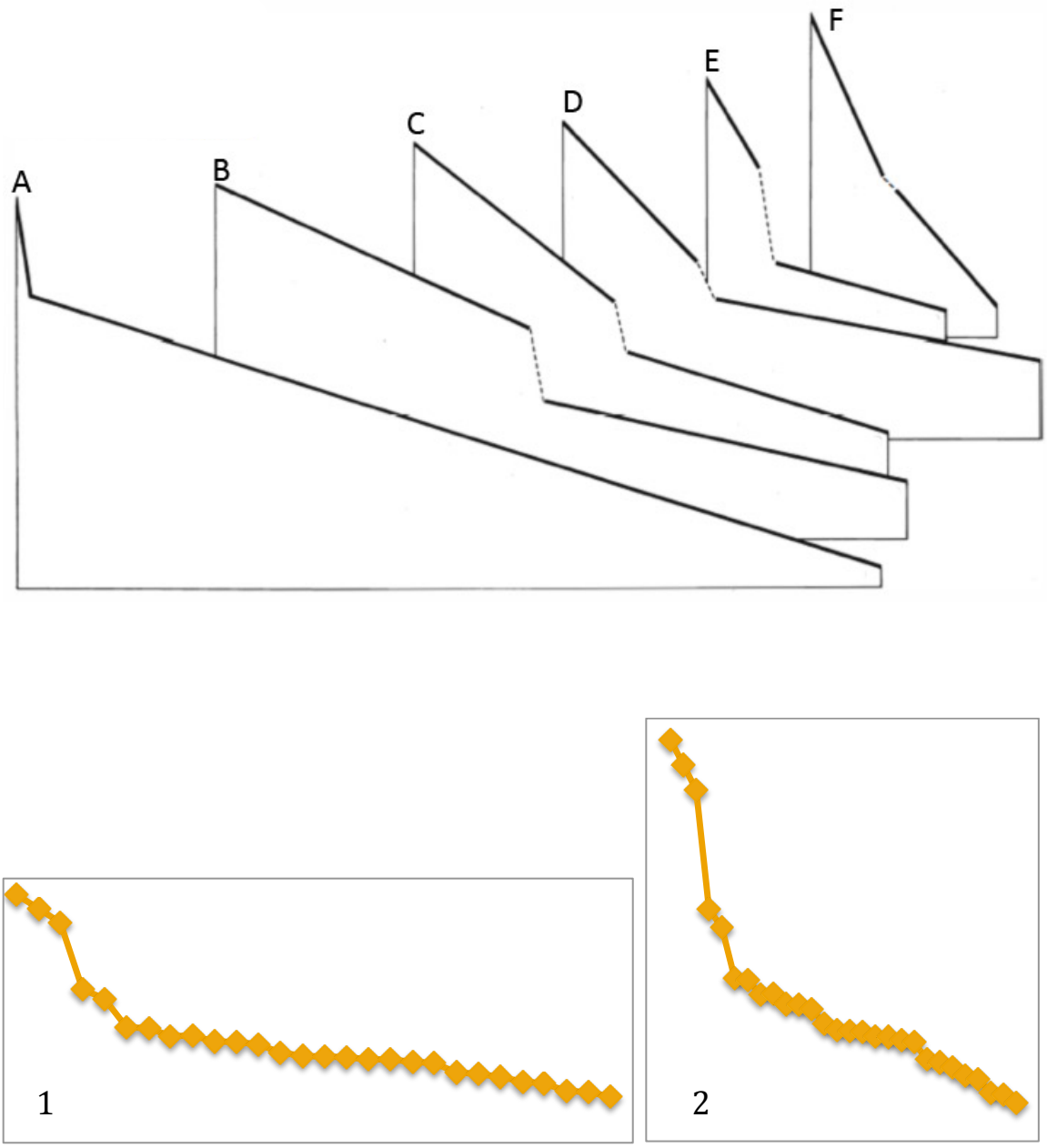


Figure 3.27. Cenograms A-F based on Legendre (1986). Cenograms 1 and 2 are from level 210-215 cm of Hall's Cave. Cenograms 1 and 2 are the same cenogram drawn with axes of different lengths.

3. Incongruity with paleoenvironmental proxies

The cenograms from the middle Holocene (Fig. 3.22), Pleistocene/Holocene transition (Fig. 3.23), and the latest Pleistocene (Fig. 3.24) are similar to the cenogram based on the modern fauna (Fig. 3.21). The main difference between those cenograms is the number of large mammals. The levels of Hall's Cave I selected to represent the middle Holocene and Pleistocene/Holocene transition only have one large mammal (*Odocoileus* sp.), and there are no large mammals preserved in the level representing the latest Pleistocene. Therefore, the general slope of the cenograms is similar to the cenogram from the modern fauna. If the cenograms are interpreted in the traditional manner, then the shallow slope of the large mammals indicates a moist environment, there is only a slight gap between the large and small mammals, taken to indicate a closed canopy, and the small mammals have a shallow slope, taken to indicate a warm environment for all these cenograms. However, this is nothing like the present environment, except that it is warm, and would indicate that the moisture level, canopy, and temperature did not change from the present until the latest Pleistocene (approximately 12 ka). This is in direct conflict with all of the proxies (Nordt et al., 1994; Musgrove et al. 2001; Cooke, 2005; Ellwood and Gose, 2006; Boulter, Bateman, and Frederick, 2010). In addition, the cenogram that could be interpreted as representing the most arid environment is from the Pleistocene, not the middle Holocene, as indicated by the independent proxies. The cenogram representing the late Pleistocene (15 ka) suggests the most arid conditions (Fig. 3.25). All independent proxies indicate this was a significantly cooler and wetter interval than the present.

I plotted all cenograms on the same graph to control for differences in number of species between the different intervals (Fig. 3.28). Visualizing the cenograms in this way shows how similar all of the Hall's Cave cenograms are. There is a slight difference

between the cenogram derived from modern mammals and that derived from late Pleistocene, but all of the cenograms look remarkably similar. The interval of time from the present to 15 ka represents a large climatic shift from full glacial conditions to present conditions. There should be a noticeable difference between Holocene and Pleistocene cenograms if they are reliable paleoenvironmental indicators.

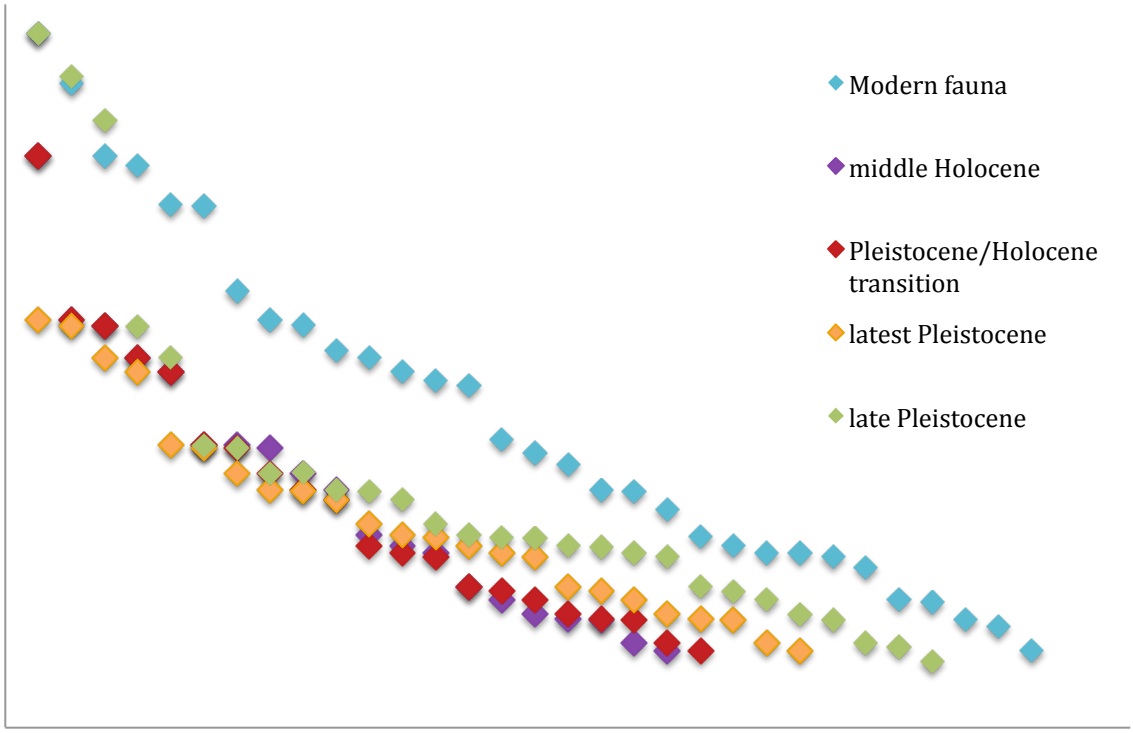


Figure 3.28. All cenograms from Hall's Cave plotted on the same axes.

Conclusions

There were no significant correlations in the species-richness models I developed for the number of frost-free days, the maximum difference in mean monthly temperature, average difference in mean monthly temperature, and maximum difference in mean monthly high temperature. This is somewhat surprising given the significant correlations found by Montuire et al., (1997), Legendre et al., (2005) and Ruez (2007) for average annual temperature. The most significant correlation in the models I developed was 0.28 for the total terrestrial mammals and maximum difference in mean monthly temperature, or 72% of the variation could be due to random chance. Mammals have a number of strategies, like migration and hibernation, to deal with seasonality. That suggests that there is the possibility that there is an artificially high correlation between the number of species of certain groups of mammals and average annual temperature or precipitation.

Cenograms and species-richness models are fraught with so many problems that they should be abandoned. Species-richness models are sensitive to taxonomic revision. If species are removed or added to a taxon used in a species-richness model, this will alter the climatic correlation. This will always be a potential source of error with the species-richness models. These models are also extremely sensitive to any bias associated with how species are identified. These models are a simple correlation with number of species. If for any reason the number of species preserved in the fossil record differs from the actual number of species that were present at a site in the past, then the data produced by the model will be inaccurate. This is a common problem with paleontological sites. The voluminous taphonomic processes that influence paleontological site formation make it probable that species will be missing from a site. Taphonomic processes will differ between sites and can change within a single deposit through time. This makes

meaningless any comparison of species-richness models between sites or through time from a single site.

Some of these problems were noted by Ruez (2007). He also found conflicting reconstructions of temperature and precipitation between the different groups of mammals from the Pliocene deposits of Hagerman Fossil Beds. He thought that the models could be improved, but that they should be adequately tested in more fossiliferous Pleistocene or Holocene sites. In addition he noted that, "Such critical evaluation should be done before application to fossil assemblages, but could also be done a posteriori to appraise previously used models and the interpretations based on them" (Ruez, 2007:340). I have shown the fundamental problems that emerge when these models are critically tested in the manner suggested by Ruez (2007).

Cenograms also are fundamentally flawed. The cenogram I plotted for the modern central Texas fauna yielded an incorrect interpretation of the present environment. This suggests that even the modern correlations are flawed in cenogram models. Most problematic is that cenograms cannot be quantified. There are no guidelines, nor standard protocols, for how they should be drawn. This allows for almost any interpretation about past environment to be made from a cenogram drawn from a paleontological deposit.

It is a worthy goal to attempt to quantify paleoecological reconstructions. Stable isotopes and radiometric dating became important tools for paleontologists in part because they allowed environmental factors and time to be quantified. However, mammals are not a physical constant like C^{14} that can be applied in a uniformitarian manner to simply extract past temperature and precipitation from paleontological assemblages. Mammals are constantly adapting and evolving in response to their environment. Although there may be significant correlations of modern mammals to

climatic parameters, it is probably an erroneous assumption that climate generally controls the distributions of mammals in a significant and consistent manner. It is impossible to document all of the biotic and abiotic factors that control the present day distribution of mammals. Therefore, it is an even greater assumption that any modern relationship between mammals and climate would be the same as the relationship during the Pleistocene or even much of the Holocene. A number of extinct vertebrate species and extralimital vertebrate taxa were present at Hall's Cave in the Pleistocene, and extralimital vertebrate taxa were found in the Holocene (Toomey, 1993). This does not include flora and much of the rest of the fauna that would have been contemporaneous. This means that any interpretations about paleoecological interactions are based on a tiny fraction the ecological activity occurring at the time the sediments of Hall's Cave were deposited.

The correlations between modern species of mammals and climatic parameters observed today appear to represent only an ephemeral phenomenon. The Hall's Cave deposit shows differences between the present-day mammalian fauna and that of just a few thousand years ago (Toomey, 1993). The direct application of correlations between modern environmental conditions and mammals is doomed to fail when applied to paleontological data. A more profitable endeavor would be to utilize independent proxy data to determine how the climatic tolerances of mammals may have changed through time.

CHAPTER 4: GIS ANALYSIS OF QUATERNARY PALEONTOLOGICAL SITES IN TEXAS: EXAMINING THE STRENGTHS AND WEAKNESSES OF THE FAUNMAP II DATABASE

ABSTRACT

I utilized GIS to analyze the factors that influence the geographic location of known Quaternary paleontological sites within Texas. The analysis was of 189 Quaternary sites from the FAUNMAP II database. Through quantitative and qualitative measures, site distribution was shown to be non-random and highly clustered. Site location is influenced by hydrography, geology, and human influenced factors. In a novel use of GIS, I analyzed the FAUNMAP II database for potential geographic bias in the identification of Quaternary fossils.

There are potential problems with the identification of Soricidae, Heteromyidae, *Odocoileus*, and *Spilogale*. For those taxa, the identification of fossils was to the generic level and only by using geography fossils identified to species. Most workers were using geographic assumptions, whether explicitly or not, to refine species identifications, and were, in effect, making generic identifications. Of special concern are taxa like *Notiosorex* and *Blarina*, for which there was only a single species recognized for most of the twentieth century. The identification of those fossils should be treated as generic identifications until they are reevaluated against the full diversity of species.

Given the problems with identifying certain species of Quaternary fossils to species I explored the potential for making paleoecologic interpretations from genera. I compared the extant ranges of shrew genera in Texas to the late Quaternary fossil record. By using independent paleoenvironmental proxies, I show that the environmental conditions found today may not be limiting the current range of shrews in Texas. If environmental conditions are not the sole factor influencing the range of shrews, then it

must be possible that other ecological factors besides the environmental conditions are shaping the current distribution of shrews.

INTRODUCTION

GIS and paleontology

Paleobiogeographic interpretations of fossils are shaped by the distribution of fossil-bearing sites and the underlying factors that influence site distribution. Although the paleontological significance of fossiliferous Quaternary-age deposits in Texas was recognized for more than a century, there was limited systematic study of the factors influencing their geographic distribution (Lundelius and Collins, 1999). Determination of the biases that affect the geographic distribution of cave and non-cave sites is the first step toward assessing the usefulness of the Quaternary fossil record for broad-scale paleoecological interpretations of fossil mammals. The development of large synthetic databases like the FAUNMAP (FAUNMAP Working Group, 1994; Graham and Lundelius, 2010) and the Neotoma Paleoecology Database (http://www.neotomadb.org/) for Quaternary localities allow for new techniques that utilize geographic information systems (GIS), and potentially can be used to make new paleoecological interpretations. GIS is an integration of software and hardware to acquire, analyze, and display geographically referenced data. GIS can display data in the form of maps, which allows for rapid querying, viewing, and interpretation of data to reveal spatial relationships, patterns, and trends. For those reasons, GIS is a powerful tool for addressing any questions that involve the spatial distribution of data.

Though GIS is widely used in other disciplines, it was slow to be adopted in paleontology. An important, early example of the use of GIS for analyzing the spatial

distribution of Quaternary mammals was done by the FAUNMAP Working Group (1996). Recent analyses concerning the spatial arrangements of paleontological sites represent a concerted effort to expand the use of GIS for the analysis of paleontological data (e.g., Fortelius et al., 2002; Rayfield et al., 2005; Conroy, 2006; Oheim, 2007; Chew and Oheim, 2009). The primary application of GIS to paleontological data is to analyze multiple datasets simultaneously and use spatial statistics to predict the potential locations of paleontological sites (e.g. Maga, 2005, Rayfield et al., 2005; Oheim, 2007). GIS also was used in non-geographic contexts to analyze fossils. Those examples include the analysis of the shape of sutures in fossil ammonites (Manship, 2004) and wear patterns in Quaternary horse teeth (George, 2003).

The goal of this paper was twofold. First, I will clarify the factors that influence geographic location of known Quaternary paleontological sites within Texas. Second, I explore the potential of using GIS to check the FAUNMAP II database for errors in the identification of fossils (Graham and Lundelius, 2010).

GIS analysis of Texas Quaternary sites

I first developed a large GIS database in collaboration with Christopher Jass to explore factors that influenced the geographic position of individual Quaternary paleontological sites within Texas, and to describe the distribution of cave and non-cave sites of different ages (Jass and George, 2010). Texas was chosen for several reasons. Although a state is an arbitrary political boundary, Texas covers a huge area (~700,000 km^2). This makes it an ideal area for studies that involve climatological and environmental questions because there is a large variation in temperature from north to south and in precipitation from east to west. The climate and elevation variation yield a

diverse range of environments (Griffith et al., 2007). Because of Texas's size it contains the maximum diversity of mammals for non-tropical United States. While political boundaries are arbitrary shapes, municipal, state and federal agencies deliver nearly all GIS data based on political boundaries.

Christopher Jass and I examined the relationship between geology, age of locality, precipitation, surface hydrology, and the distribution of cave and non-cave sites over a restricted geographic region (Texas), the null hypothesis being that site distribution was random (Jass and George, 2010). We used GIS to analyze locality data from a combined database of FAUNMAP (FAUNMAP Working Group, 1994) and the unpublished locality records of the Vertebrate Paleontology Laboratory (VPL) at the Texas Memorial Museum. In Texas, there is a strong geographic influence on site location related to local surface geology and surface hydrology, and there is a difference in the distribution of cave versus non-cave sites (Jass and George, 2010). Most of the caves are found on the Edwards Plateau, the large carbonate-rich region of central Texas. This is a karst area, and includes sinkholes, caves, and springs. It is generally covered by little soil, and over the entire region, there are limited sediments, making non-cave sites rare. Although non-cave sites are broadly distributed across all of Texas, they are most common in east and north Texas where there are large accumulations of sediments, and the sites coincide with Quaternary alluvium. There is a close relationship between local surface hydrology and Quaternary sites in Texas, and both cave and non-cave sites are common along current or past rivers and streams. We compared site location with precipitation maps and level III and IV ecoregions (Griffith et al., 2007), but we were unable to discern a quantifiable relationship between site location and either of these environmental variables (Jass and George, 2010).

We found that caves make a significant contribution to improving the coverage of Quaternary fossil sites (Jass and George, 2010). Time intervals or geographic regions that do not preserve cave deposits are likely to yield more biased interpretations of species richness, paleoecology, and paleobiogeography. Caves often preserve more diverse faunal assemblages than other Quaternary sites. Therefore, comparing areas where caves are common to an area without caves (or similarly taxon-rich assemblages) could lead to seriously prejudiced interpretations of paleoecology or the changes in taxon distributions. Attention should be paid to the spatial relationship of different types of sites to verify that the data are comparable in taxonomic and geographic sampling (Jass and George, 2010).

Potential and pitfalls of FAUNMAP databases

During a previous study (Jass and George, 2010), we noted that there is tremendous potential for asking many paleontological questions from large datasets, such as FAUNMAP. However, the results of any inquiry using them are dependent on the quality of the data in the database. Other analyses of the FAUNMAP database were of the large-scale organization and distribution of mammals during the Late Pleistocene in the continental United States (FAUNMAP Working Group, 1996; Lyons, 2003; Cannon, 2004; Lyons, 2005). Those studies included GIS analysis of range shifts of mammals from approximately 40 ka to 500 years ago. The FAUNMAP Working Group found that many taxa were found in non-analog assemblages in the Pleistocene. Essentially, this means that the species that are today separated by hundreds of miles or more were found in association in Pleistocene deposits, so that mammals found today in incompatible habitats were found together. The conclusion reached by the FAUNMAP Working Group was that species responded in a Gleasonian (individualistic) manner to climate

change over the last glacial-interglacial transition. They found that though individual species might have responded to climate change in idiosyncratic ways, the larger scale biotic provinces remained intact from the Late Pleistocene to the Holocene (FAUNMAP Working Group, 1996).

In more recent analyses, the relationship between species distributions and climate was found to be more complex (Lyons, 2003; 2005), and that not all communities would be non-analogue. Lyons conclusions were that although species were responding to climate change individualistically, species associations persisted through time because the environmental preferences of species remained similar (Lyons; 2005). Neither her analyses nor the analysis by the FAUNMAP Working Group (1996), took into account a potentially significant bias of the data in the FAUNMAP database. Their conclusions were dependent on the accurate identifications of species of fossils.

If geography was used to aid in the identification of species, then the studies were biased. Another potential bias to their conclusions would result if sites are not evenly distributed across the continental United States. By working at a large geographic scale (continental United States), problems with uneven site distribution would be minimized, and both Lyons and the FAUNMAP Working Group discussed this issue. However, the quality of fossil identifications remains a major concern, and was unaddressed.

The use of geographic or temporal assumptions to restrict the pool of species or specimens compared is common for Quaternary-age fossils (Bell et al., 2010). Using geography to supplement morphologic similarities in order to refine identifications is a hidden assumption that is often not explicitly stated in the description of how fossils were identified. Though common, this can impede or eliminate the ability to detect range shifts of taxa through time. While it is possible that using geography to supplement the identification of species is not a systemic problem, the fact that large shifts in the range of

species were recognized from the Pleistocene to the Holocene (FAUNMAP Working Group, 1996; Lyons, 2003; Lyons, 2005) may indicate that only when there is a significant difference in time or location were faunal changes recognized. If it is assumed that there was little change in Holocene faunas, then it is unlikely that much effort would go into comparing species from a wide geographic range. Another potential bias could be in the direction mammals were assumed to disperse due to climate change. It was long assumed mammals dispersed north and south during the Pleistocene because of repeated continental glaciation (e.g., Buckland, 1822; Matthew, 1915). Not all dispersal will be driven by changes in mean annual temperature, but if paleontologists work from the perspective that temperature change is the primary agent of dispersal, it will bias the recognition of faunal turnover. Though there are many serious reasons to recognize and prevent geographical bias in the identification of fossils, there are only limited attempts to document this potential problem (Stewart, 2005; Bell et al., 2010).

I began this study to determine if GIS could be used to investigate Quaternary paleoecology. Because GIS analysis uses spatial relationships, I first ascertained which factors influenced the location of Quaternary sites. Presumably, Quaternary site distribution is non-random. Previous work (Jass and George, 2010) indicated that factors such as geology, age, precipitation, or hydrography influence site location, and as a natural extension of this work, I wanted to better quantify those properties that regulate site distribution.

If Quaternary sites are randomly distributed across Texas, then there will be no correlation to any geographic features. To test the hypothesis that site distribution is non-random, I quantified the distribution of sites relative to average annual precipitation, ecoregions, roads, and proximity to drainage features. The GIS analysis by Jass and George (2010) only included the distribution of sites in Texas, but did not consider the

fauna from the sites. To build upon this work, I wanted to determine where geography might have influenced species identification. The first approach I took to determine if geography played a role in identification was a taxonomic expert point of view. My expertise in identifying shrews (Chapter 2) was used to assess which identifications of shrew species were potentially problematic. A second novel approach, which I develop here, was to use GIS to help find fossils that were potentially identified to species based on geographic assumptions.

Another question I explore is if species identifications are inaccurate or impossible without geographic assumptions, then what is the potential for using taxonomic levels above the species level to make paleoecological interpretations? To explore the potential for paleoecological interpretations above the species level, I looked at the shrews from Quaternary sites in Texas. Shrews are a common taxon in paleoecologic analyses (e.g., Graham and Semken, 1976; Klippel and Parmalee, 1982; Toomey et al., 1993), and are an apt taxon for determining if generic identifications yield different interpretations than species identifications. There are a number of genera with overlapping extant ranges, there are good morphological characters that separate genera (Chapter 2), and there are preexisting paleoecological interpretations for comparison.

This study represents the first steps towards using GIS to make paleoecologic interpretations about Quaternary mammals. My ultimate goal is to utilize GIS to test predictions of the effect of paleoclimate on Quaternary mammals. It is important at this stage to address the potential biases within the FAUNMAP database, such as the distribution of sites and the identification of fossils. Once these problems are addressed and more independent paleoenvironment data are available and integrated into the GIS database, further analysis will yield a more comprehensive picture of how climate change during the Quaternary affected mammals.

Materials and Methods

The Quaternary site data came from the FAUNMAP II database (Graham and Lundelius, 2010). A list of the FAUNMAP II sites from Texas used in this analysis is provided in Appendix C. The FAUNMAP I database only includes sites that were radiocarbon dated. Those sites are roughly less than 50,000 years old. The age range of sites was extended to include all of the Pleistocene, as well as the sites in FAUNMAP I, in the FAUNMAP II database. For the analysis, I relied upon the depositional systems (cave vs. non-cave), the relative age of the faunas, the numeric age dates (in radiocarbon years, not as calibrated ages), and the taxonomic data as listed in the FAUNMAP II database.

There were 189 Quaternary sites from Texas in the FAUNMAP II database. Of those, 55 were cave sites. The depositional systems were classified in the FAUNMAP II database as lacustrine, fluvial, gravity, aeolian, cave, spring, volcanic, marine, biological, and anthropogenic. All depositional systems other than caves were treated collectively as non-cave sites.

All other digital data included in the GIS analysis came from publicly available online data sources. The geologic data came from the United States Geological Survey (http://tin.er.usgs.gov/geology/). Hydrography (streams and rivers) data are from the Texas Water Development Board (http://www.twdb.state.tx.us/). These data are the major rivers that were extracted from the National Hydrography Dataset at 1:100,000 scale. The road data of all public roads in Texas, and the Texas county data came from Texas Natural Resources Information System (http://www.tnris.org). The ecoregions and average annual precipitation data came from Texas Parks and Wildlife (http://www.tpwd.state.tx.us). The historical areal distribution data of extant mammals came from natureserve.org (Patterson, et al., 2007). Selected point data of extant shrew

specimens came from the Mammal Networked Information System (MaNIS, http://manisnet.org/).

I conducted the GIS analysis using ESRI ArcGIS version 9.2. In an effort to explore the factors that influenced the geographic distribution of Quaternary sites, I evaluated a number of characteristics. A strength of GIS is that is permits the combination of a number of different types of data, and can analyze them concurrently (Figure 4.1). Starting with a base map of Texas, I added Quaternary site data from FAUNMAP II. I then examined the relationship between precipitation, hydrography, ecoregions, and geology and the distribution of cave and non-cave sites across Texas; the null hypothesis was that site distribution was random.

To test if site distribution was random, I calculated the average nearest-neighbor test statistic using the ArcGIS 9.2 average nearest-neighbor tool. The statistic is calculated by measuring the distance between each feature and its nearest neighbor and then averaging all the distances between features. The test statistic is a comparison of the mean of the distance observed between each point and its nearest neighbor to the expected mean distance that would occur if the distribution were random. Distributions that have a smaller average distance between features than a random distribution are considered clustered, and distributions that have a greater average distance between features than random are considered dispersed.

I also tested for directional bias in the distribution between cave and non-cave sites. To capture the shape of the distribution I generated a standard deviational ellipse for both cave and non-cave sites using the standard deviational ellipse tool in ArcGIS 9.2. A standard deviational ellipse represents one standard deviation, or 68% of the features. The major axis of the ellipse defines the direction of maximum spread of the distribution. The minor axis is perpendicular to it and defines the minimum spread.

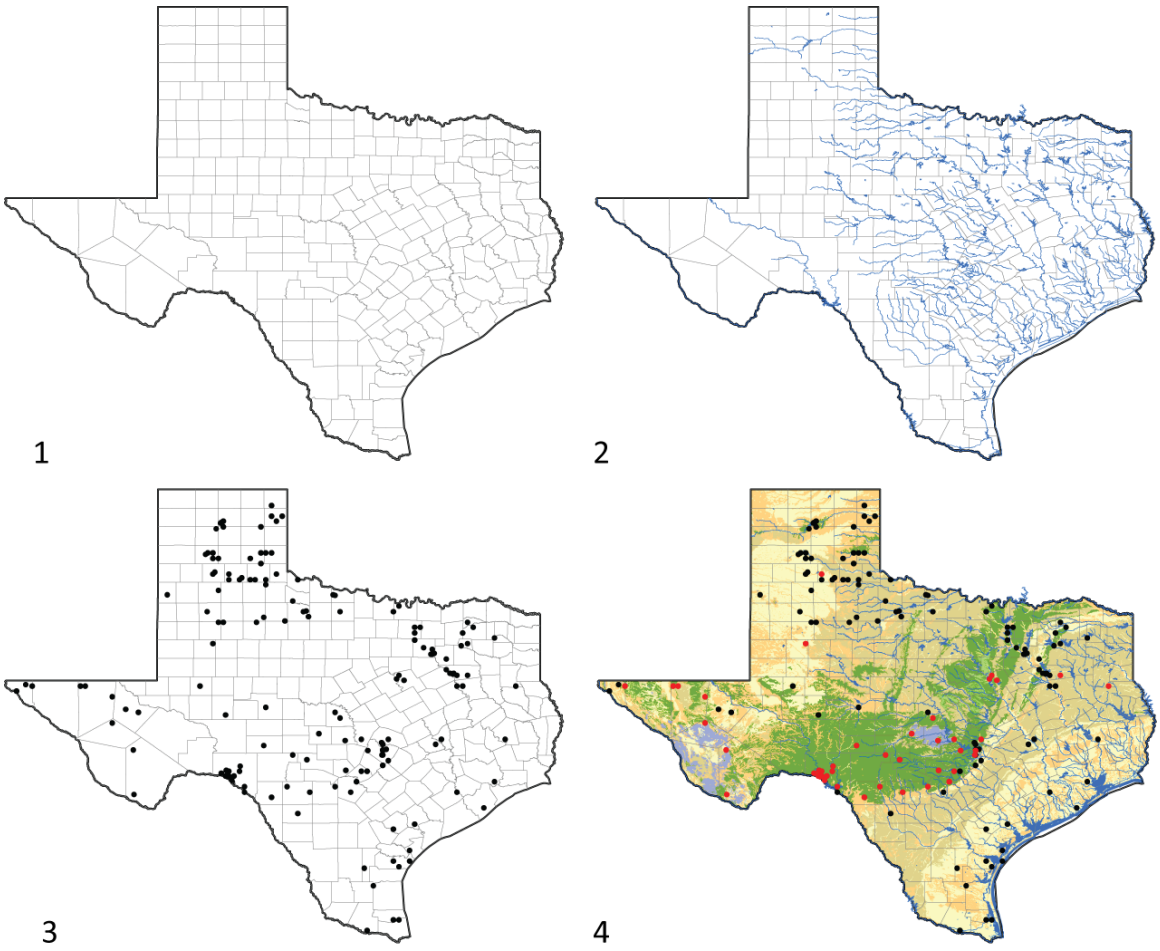


Figure 4.1. Sequential additions of data allow for the geographic analysis of multiple data sets. 1. Base map of Texas. 2. Addition of rivers. 3. Quaternary sites. 4. Combined GIS database with geology, rivers, and Quaternary sites shown with cave (red) and non-cave sites (black).

To analyze the effect of precipitation on site distribution, I took the map of average annual precipitation from 1961-1990 (http://www.tpwd.state.tx.us), and ArcGIS grouped the data into ten bins representing the range of precipitation. I used the Count Points in Polygons tool from Hawth's Analysis Tools for ArcGIS (Beyer, 2004) to quantify differences between the number of cave and non-cave sites per bin of precipitation. The Count Points in Polygons tool was also used to quantify differences between the number of cave and non-cave sites per ecoregion in GIS. The ecoregions are demarcated by shared flora, fauna, and physiography. I used level three ecoregions (sensu Griffith et al., 2007).

The discovery of fossil localities is driven by access and opportunity; roads and streams afford both. Roads and streams provide the means to get to a site, and stream erosion and road construction will expose fossils. I tested the correlation of Quaternary sites in Texas to rivers and roads through a proximity analysis. I created buffers of 10 m, 100 m, 500 m, 1500 m, and 10,000 m around each of the sites using the proximity tool ArcGIS 9.2 Toolbox. The sites are point data in GIS, and applying a buffer gave them the dimensions of a circle with a radius the length of the buffer. I could then test each buffer to determine which sites were within a given distance of a road or river.

In an effort to identify situations in which the geographic range of extant taxa may have been used to help identify fossils to species, I took modern mammal distributions and overlaid Quaternary sites with fossils identified to the same genus. I selected taxa from three separate orders of Mammals in addition to the shrews. I queried the FAUNMAP database for deer (Artiodactyla: *Odocoileus*), pocket mice and kangaroo rats (Rodentia: Heteromyidae), and spotted skunks (Carnivora: *Spilogale*). These taxa were selected because they are difficult to identify to species from isolated skeletal material and there are significant differences in the geographic ranges of the species within a genus.

RESULTS

Site distribution analysis

The average nearest-neighbor test demonstrated that Quaternary sites in Texas are not randomly distributed. The sites have a highly clustered distribution. The test statistic of the average nearest neighbor test indicated that there is less than a one percent chance that the sites are spatially random. Sites are not randomly distributed across Texas, and there are many factors that group sites together. Foremost of the factors is that once a site is found paleontologists would go back and look in the same area for more sites. Beyond that, there are a number of other factors influencing site distribution.

I first looked at the difference in distribution of cave and non-cave sites using the standard deviational ellipse tool in ArcGIS 9.2. There are clear differences in the spread and orientation between cave and non-cave sites (Figure 4.2). The ellipses shown in Figure 4.2 are drawn by ArcGIS with the center of the ellipse at the centroid of all the points. The long axis of the ellipse is oriented in the direction of majority of sites. The rounder the ellipse, the more even the distribution of sites around the centroid. The ellipse encloses 68% of the sites. The ellipses make it visually easier to focus on the majority of sites. Most of the distribution of cave sites is centered in central Texas around the Edwards Plateau. This is a karst area, so it is unsurprising that most of the caves are found there. The majority of the non-cave sites are located to the north and east in Texas.

To further refine the factors controlling site distribution I quantified the difference between the distribution of cave and non-cave sites and average annual precipitation (Table 4.1). There is a strong east-west moisture gradient in Texas between the arid west and humid east (Figure 4.3). There are few caves in the areas of high mean annual precipitation, and the largest percentage of cave sites are in the arid regions. The largest number of cave sites is found in the area with 18-23 in. of annual precipitation, but

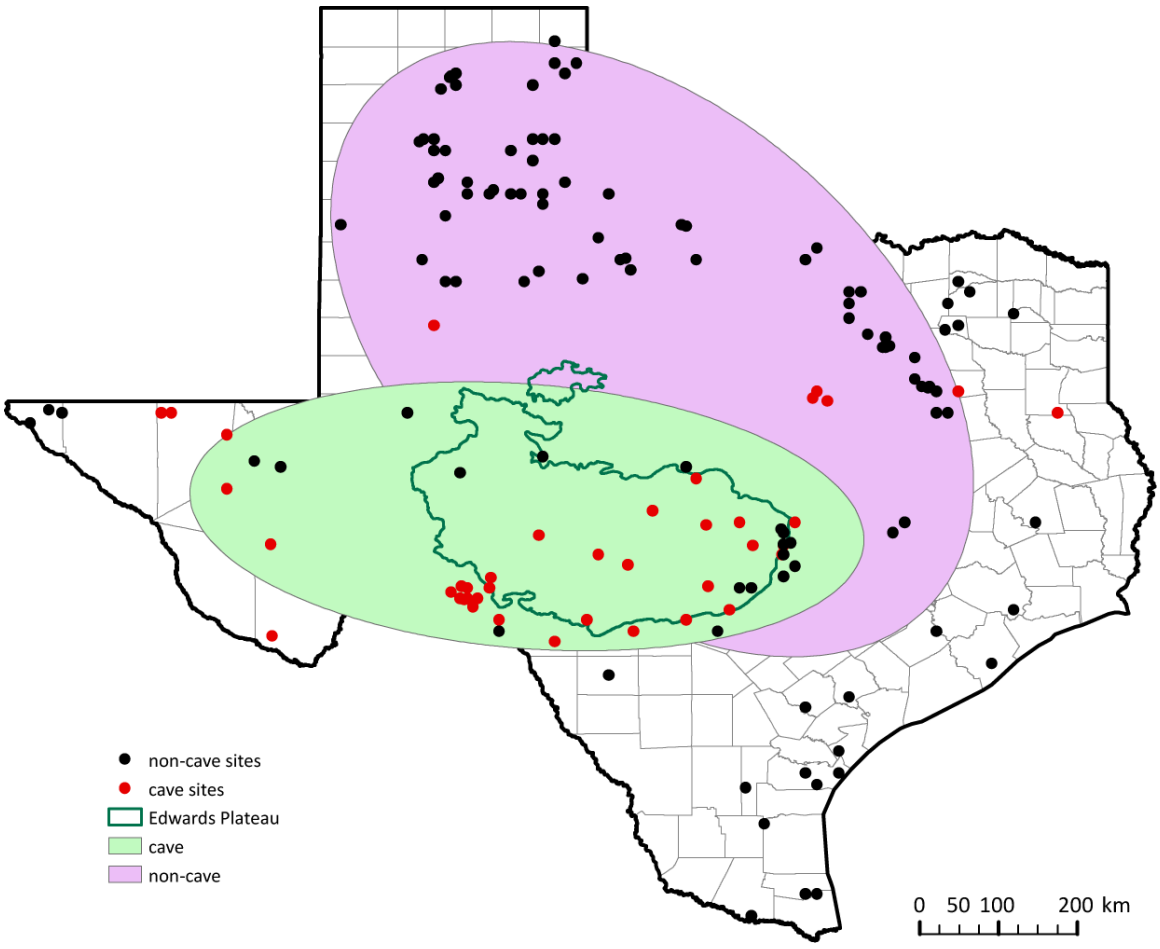


Figure 4.2. Standard deviation ellipses of cave and non-cave. These ellipses cover 68% of the sites and show the major orientation of the distribution of sites.

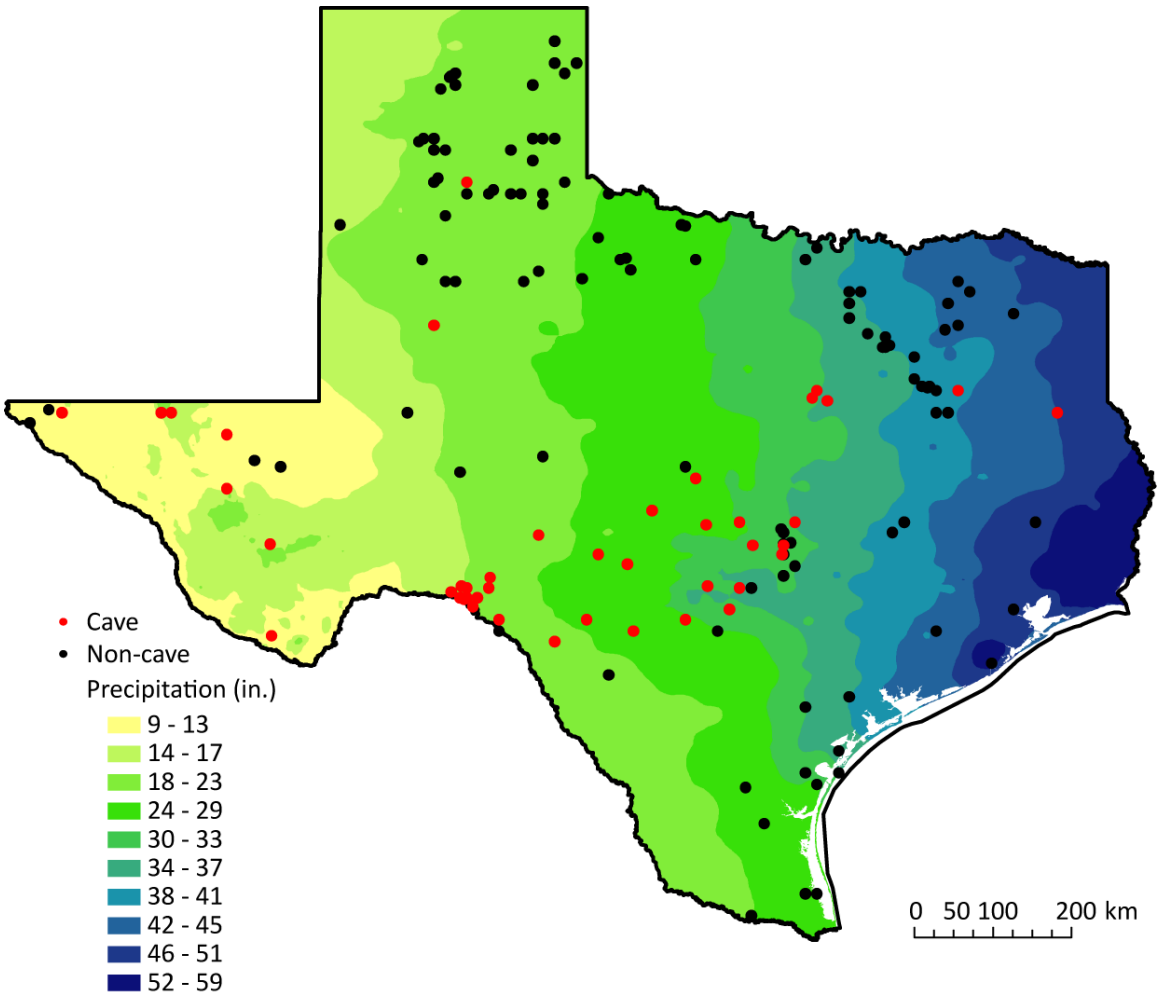


Figure 4.3. Average annual precipitation in inches shown with Quaternary sites.

there are also a large number of non-cave sites as well (Table 4.1). In the other arid areas, there are few Quaternary sites in total. The high proportion of cave sites in those regions is likely due to the low number of sites rather than an intrinsic relationship between the presence of caves and low precipitation.

Table 4.1. Number of Quaternary sites found in zones of a given range of average annual precipitation. The proportion is the percentage of cave sites.

Precipitation (in.)	# of cave sites	# of non-cave sites	Proportion of caves as %
9 to 13	5	7	42
14 to 17	10	2	83
18 to 23	12	56	18
24 to 29	11	19	37
30 to 33	8	10	44
34 to 37	3	14	18
38 to 41	1	16	6
42 to 45	1	8	11
46 to 51	0	2	0
52 to 59	0	2	0

There are quantitative differences between the numbers of Quaternary sites in the various ecoregions of Texas (Table 4.2). There are 12 Level III ecoregions in Texas. The Level I ecoregions are the largest in scale, dividing North America into 15 ecological regions. Level 3 were developed for land management agencies to provide regional-scale ecosystem classifications (Griffith et al., 2007). The Arizona/New Mexico Mountains, Chihuahuan Desert, and Edwards Plateau ecoregions had the largest proportion of cave sites. The Arizona/New Mexico Mountains are the smallest ecoregion. That ecoregion

represents the Guadalupe Mountains that extend into Texas along the southern New Mexico border midway between El Paso, TX and the western edge of the Panhandle (Figure 4.4). Caves are relatively rare in the plains ecoregions. Ecoregions are in part defined by the geology of the region (Griffith et al., 2007). The geology is more significant in determining location of cave sites than other ecological factors (Figure 4.5). Caves are most common in the large carbonate-rich region of central Texas known as the Edwards Plateau. Other Quaternary sites are most common in east Texas and the Panhandle and show a broad distribution across all of Texas, corresponding to areas mapped as Quaternary alluvium.

Table 4.2. Number of Quaternary sites found in each ecoregion. The proportion is the percentage of cave sites.

Ecoregion	# of cave sites	# of non-cave sites	Proportion of caves as %
Arizona/New Mexico Mountains	1	0	100
Central Great Plains	0	14	0
Chihuahuan Deserts	20	7	74
Cross Timbers	3	6	33
East Central Texas Plains	1	14	7
Edwards Plateau	16	5	76
High Plains	2	16	11
South Central Plains	1	2	33
Southern Texas Plains	2	1	67
Southwestern Tablelands	0	35	0
Texas Blackland Prairies	5	22	19
Western Gulf Coastal Plain	0	14	0

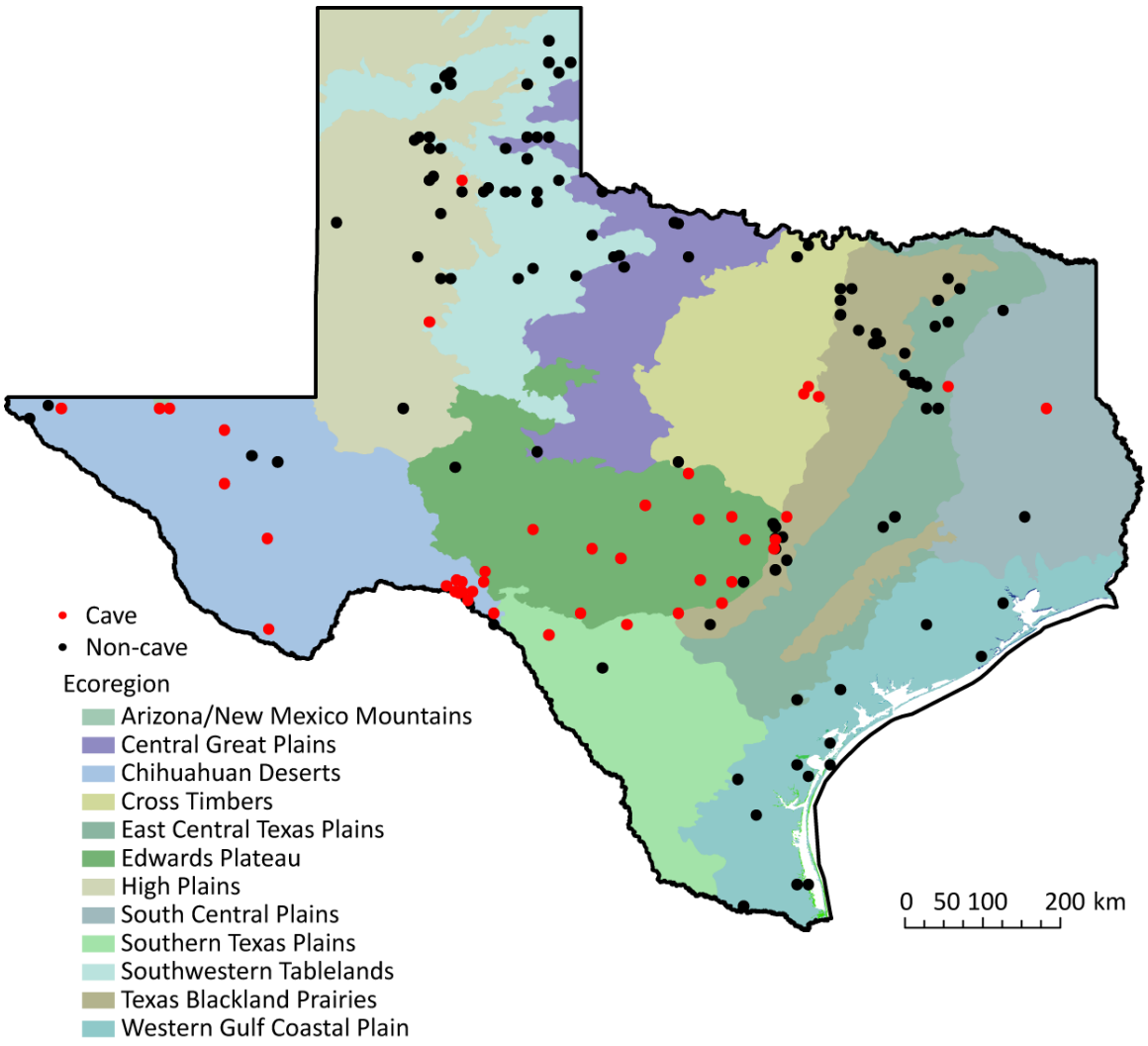


Figure 4.4. Map of the ecoregions of Texas (Griffith et al., 2007) with Quaternary sites.

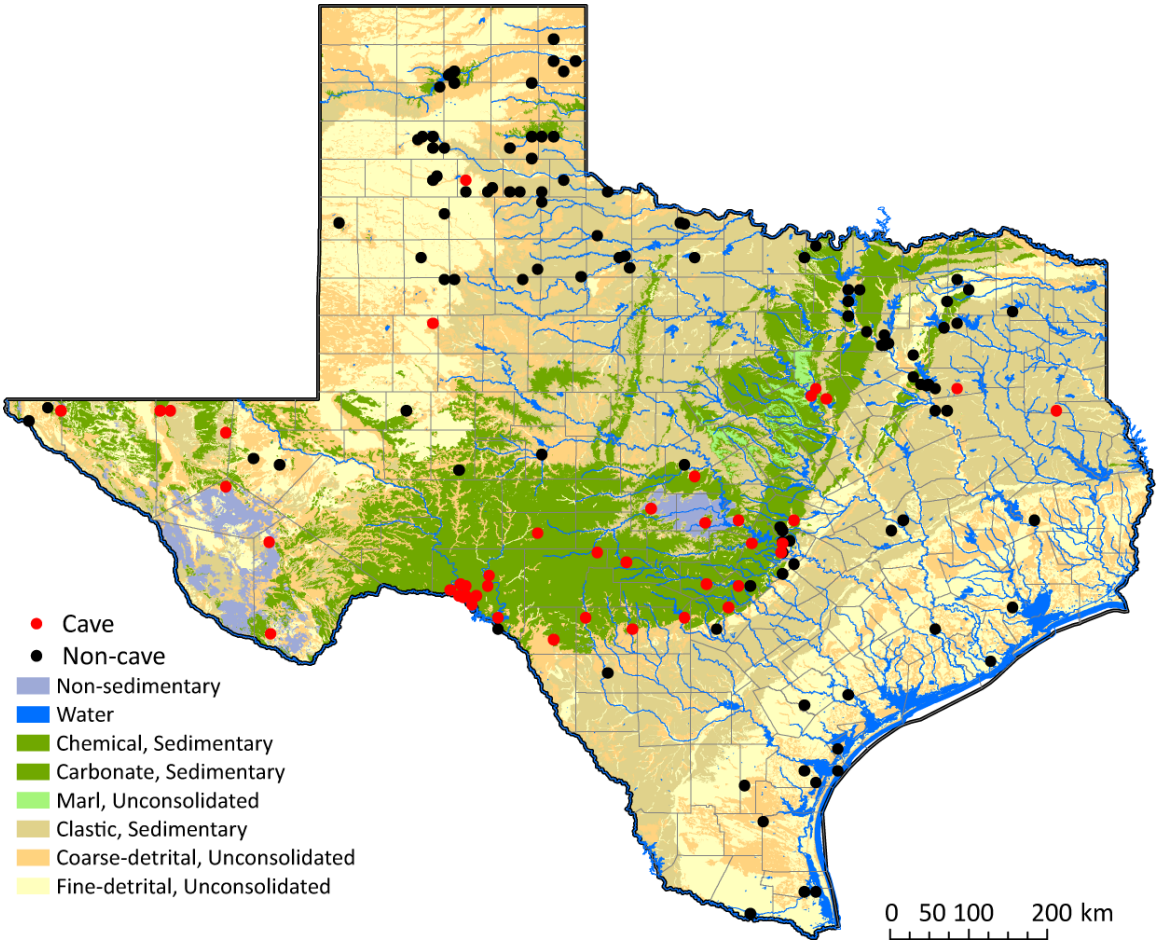


Figure 4.5. Quaternary sites shown with underlying geology.

There are two strong geographic influences on Quaternary site location. First is hydrography (Figure 4.6). The river data are 1:100,000 scale, which is broad scale, and does not include smaller streams and minor tributaries. However, there is a correspondence of Quaternary sites to streams and rivers, and this is particularly true for non-cave sites. The numbers of sites that are found with the proximity classes I defined are found in Table 4.3. Within 10 m of rivers there were no Quaternary sites. There are a roughly equal proportion of cave and non-cave sites at each distance from the rivers (Table 4.3). This indicates that there is not a strong predilection for either type of site to be found near rivers.

The other major influence on Quaternary site location is the proximity to roads (Figure 4.7). The proximity of roads to sites is summarized in Table 4.4. There are a few sites found within 10 m of roads. No additional cave sites were identified when the buffer size was increased to 100 m. At that proximity, cave sites are underrepresented compared to non-cave sites. All Quaternary sites were within 10,000 m of roads.

Table 4.3. Quaternary sites in proximity to rivers

	# of cave sites	# of non-cave sites	Proportion of caves as %
100m	1	4	25.0
500m	5	23	21.7
1500m	14	43	32.6
10000m	33	130	25.4
Total	55	189	29.1

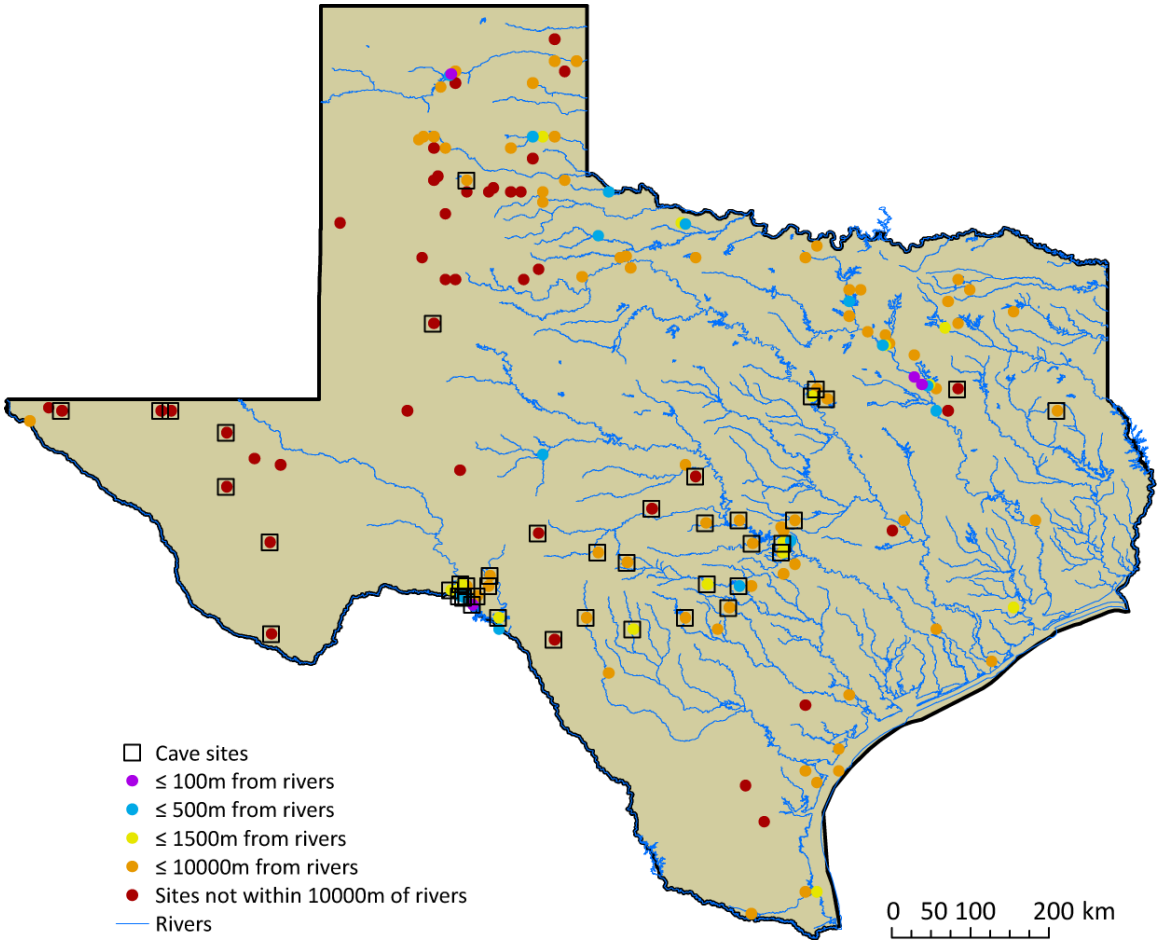


Figure 4.6. Hydrography shown with the Quaternary sites color-coded by proximity to rivers.

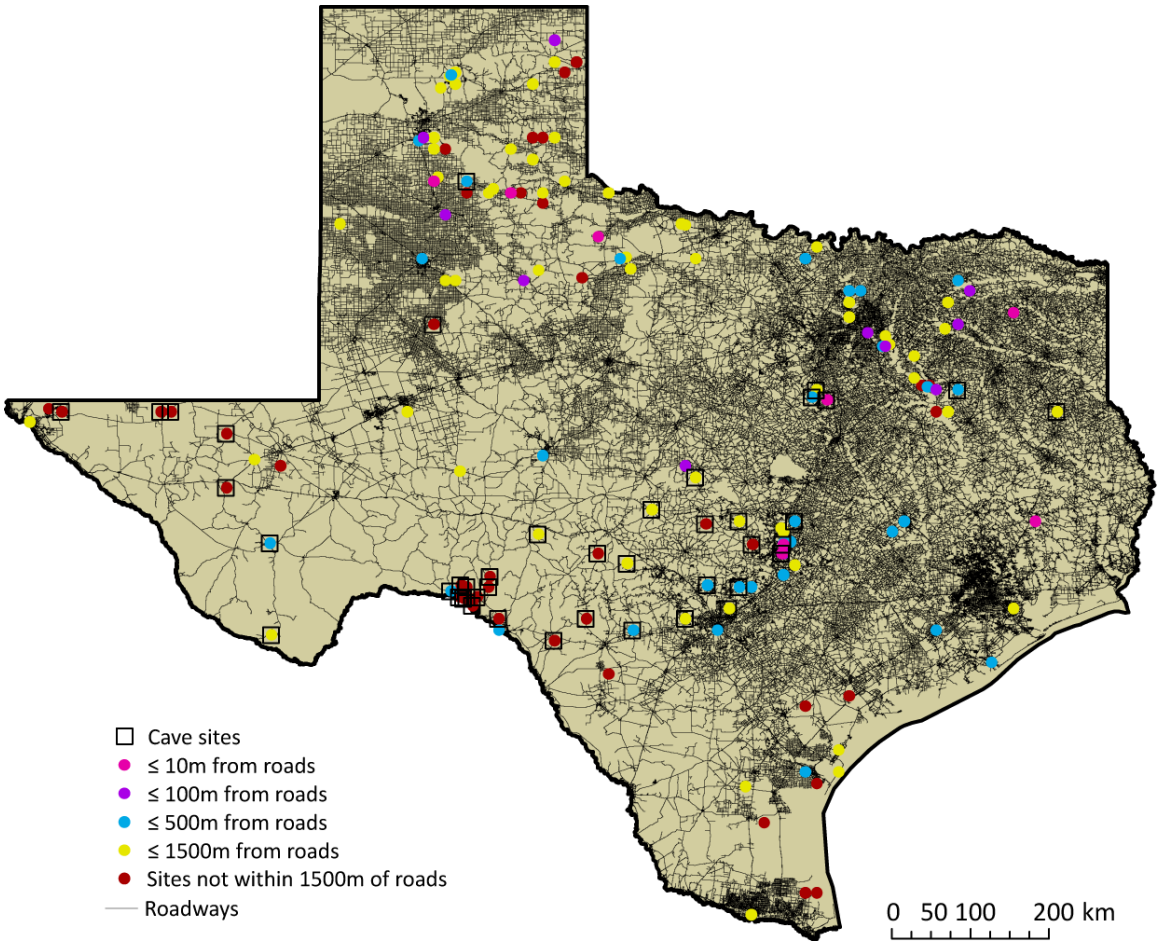


Figure 4.7. Quaternary sites color-coded to their proximity of paved roads.

Table 4.4. Quaternary sites in proximity to roads.

	# of cave sites	# of non-cave sites	Proportion of caves as %
10m	4	9	44.4
100m	4	23	17.4
500m	14	61	23.0
1500m	24	132	18.2
Total	55	189	29.1

Analysis of geographic bias in identification

The modern distribution of shrews covers almost the entire state of Texas (Figure 4.8). Most of the coverage is from two species, *Notiosorex crawfordi* and *Cryptotis parva*. *Notiosorex crawfordi* is the only species of Notiosoricini found in Texas today (Figure 4.9). *Cryptotis parva* is a member of Blarinini. The other species of Blarinini found in Texas today are *Blarina carolinensis* and *Blarina hylophaga* (Figure 4.10). The species of *Blarina* do not expand the range of shrews and are completely overlapped by *Cryptotis parva*. *Blarina* and *Cryptotis* overlap throughout most of their range. *Sorex* is not found in Texas today.

Figure 4.11 is a map of the Quaternary sites, with sites containing shrews shown as diamonds. 45 sites are reported to contain fossil shrews (Table 4.5). Of those, 19 are cave sites. Only 14 sites that contain shrews are Post-Rancholabrean in age. There is a greater diversity of shrew species in the Pleistocene than is found in Texas today (Table 4.5).

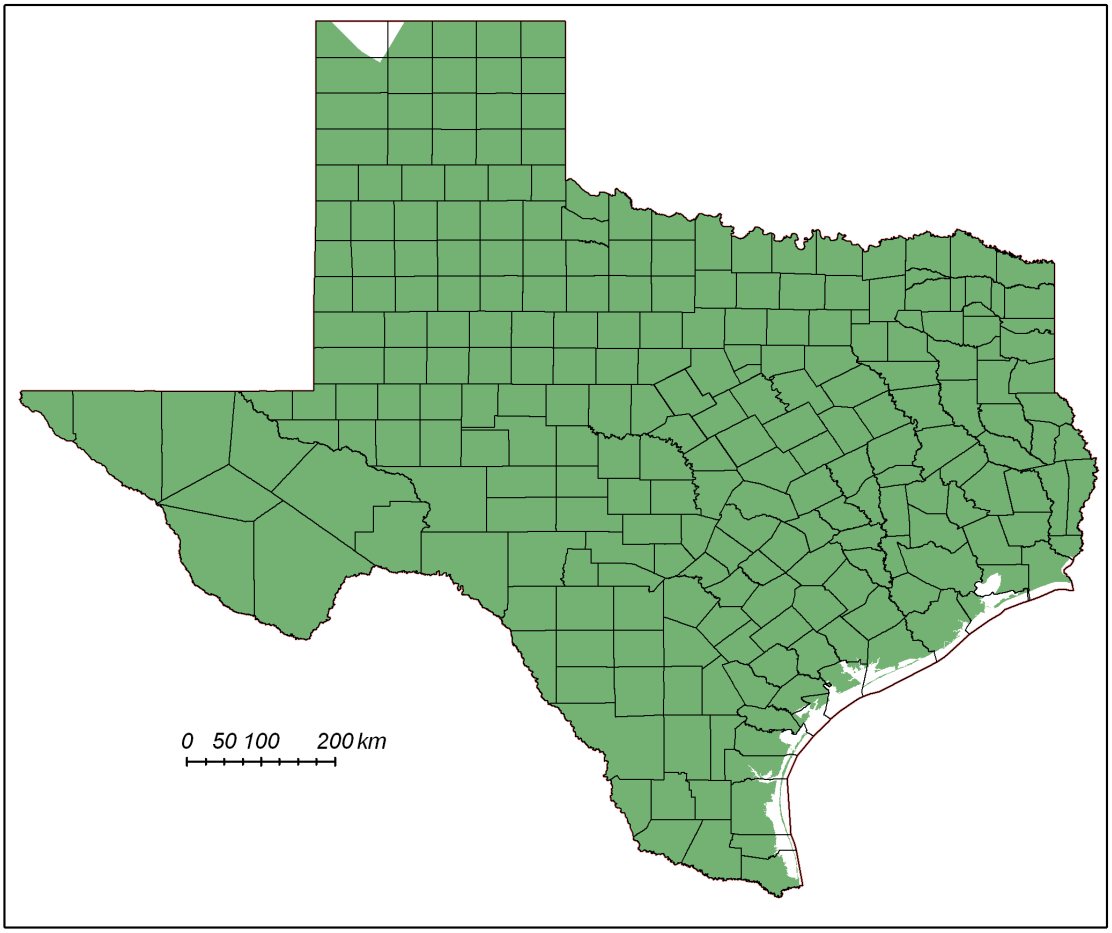


Figure 4.8. Modern distribution of Soricidae in Texas. This was derived by combining the ranges of the modern species of shrews found in Texas.

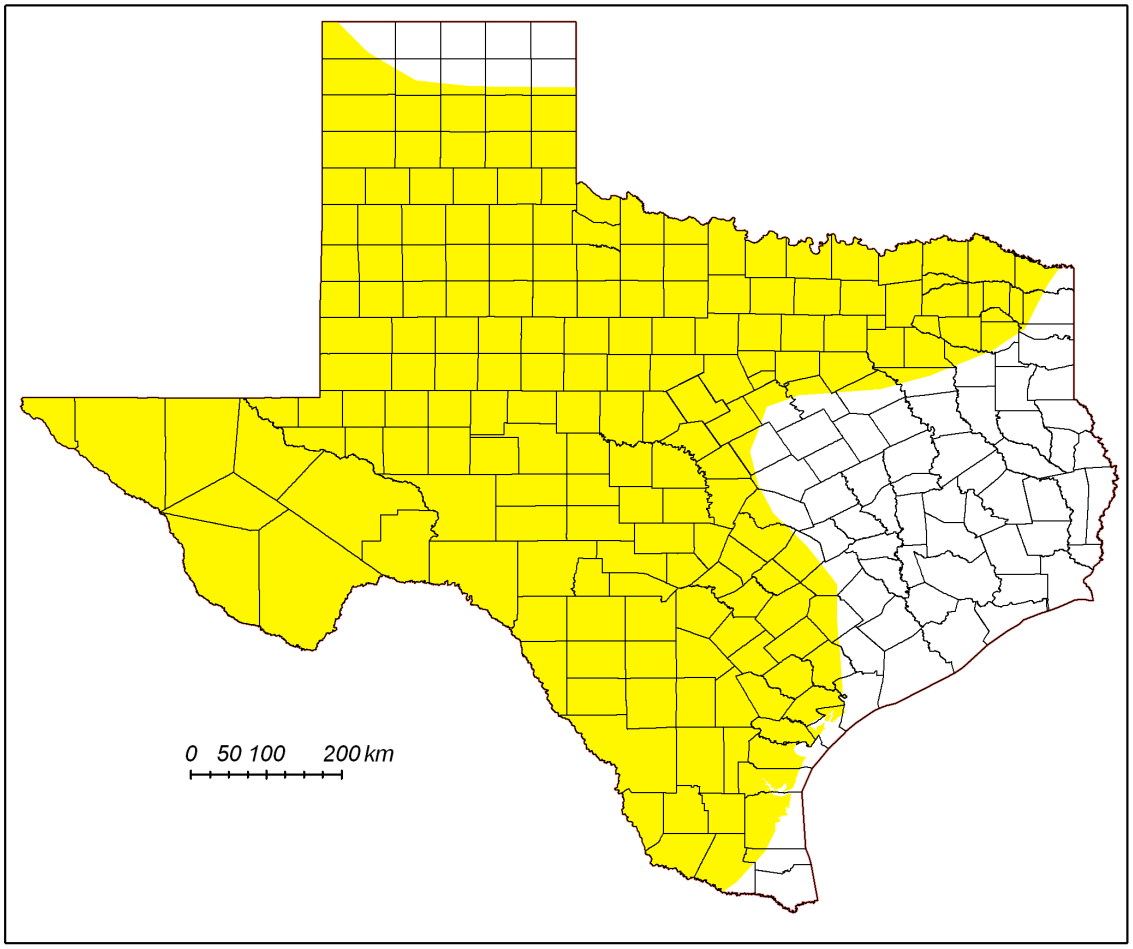


Figure 4.9. Modern distribution of *Notiosorex crawfordi* in Texas.

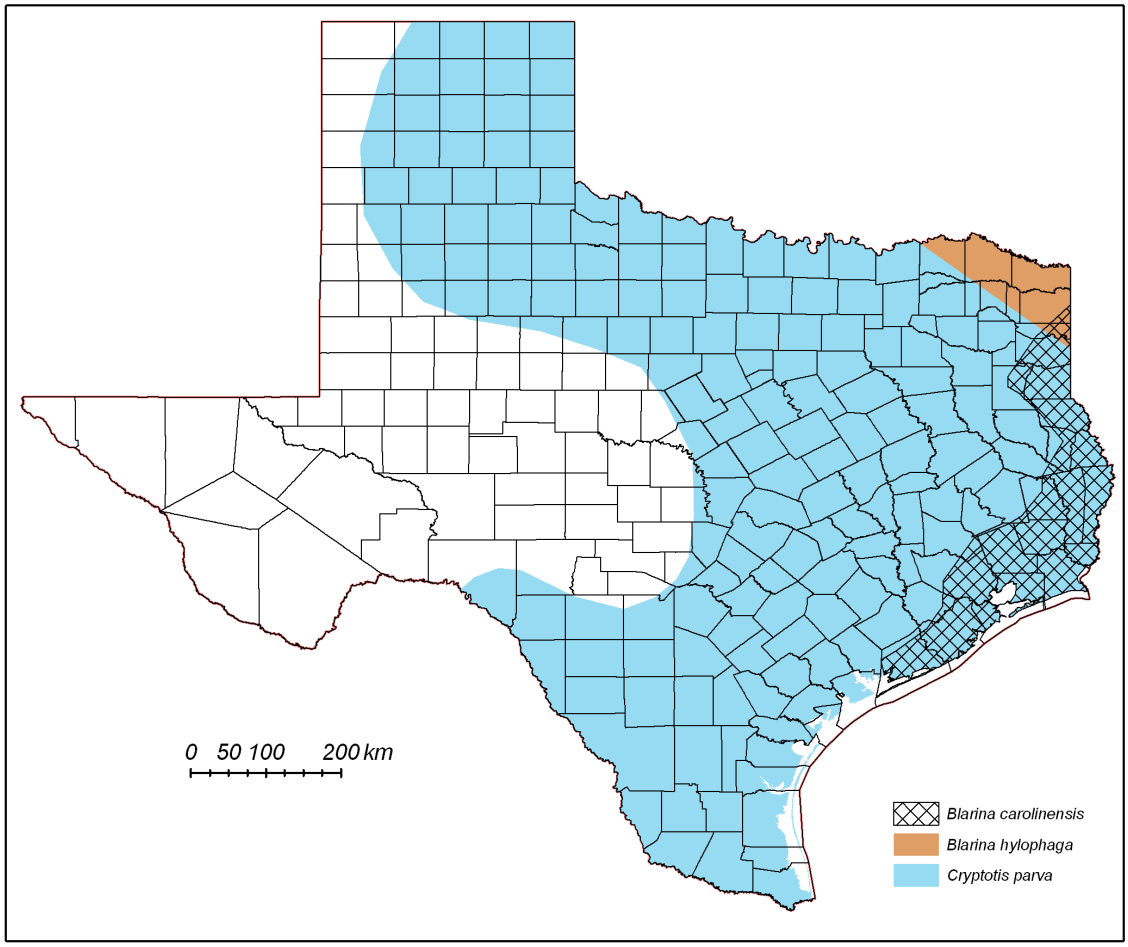


Figure 4.10. Modern distribution of Blarinini in Texas.

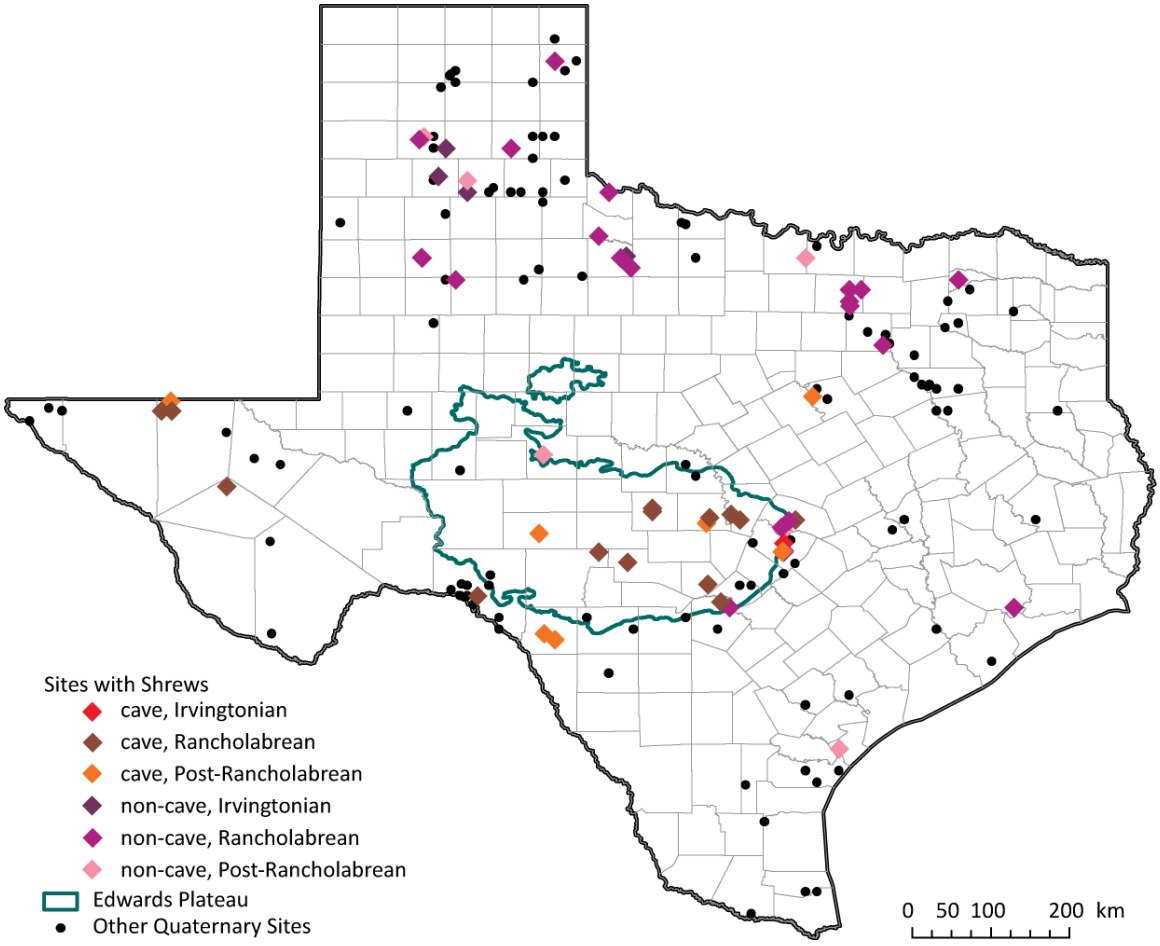


Figure 4.11. Quaternary sites in the FAUNMAP II database with shrews are shown as diamonds. All other Quaternary sites shown as black dots.

Table 4.5. Table of Quaternary sites and the excavation units with shrews.

Site Name	Excavation Unit	Genus	Species	Age of Fauna
41TG91	Area A Zone 3	*Cryptotis*	*parva*	Post-Rancholabrean
41TG91	Area A Zone 3	*Notiosorex*	*crawfordi*	Post-Rancholabrean
41TG91	Area A Zone 4/7	Soricidae	unid	Post-Rancholabrean
Aubrey	Pond	Soricidae	unid	Rancholabrean
Aubrey	Spring	Soricidae	unid	Rancholabrean
Avenue	Area B	*Blarina*	*carolinensis*	Rancholabrean
Avenue	Area B	*Cryptotis*	*parva*	Rancholabrean
Barton Road	Cultural Unit	*Blarina*	*carolinensis*	Post-Rancholabrean
Barton Road	Cultural Unit	*Cryptotis*	*parva*	Post-Rancholabrean
Barton Road	Cultural Unit	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Barton Road	Non-Cultural Unit	*Cryptotis*	*parva*	Post-Rancholabrean
Barton Road	Non-Cultural Unit	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Beck Creek Local Fauna	Assemblage	*Cryptotis*	*parva*	Rancholabrean
Ben Franklin	Assemblage	*Blarina*	sp.	Holocene/Pleistocene
Ben Franklin	Assemblage	*Sorex*	*cinereus*	Holocene/Pleistocene
Bull Draw Local Fauna	Assemblage	*Sorex*	*cinereus*	Irvingtonian
Bull Draw Local Fauna	Assemblage	*Sorex*	*lacustris*	Irvingtonian
Bull Draw Local Fauna	Assemblage	*Sorex*	*megacephalus*	Irvingtonian
Canadian Local Fauna	Site 26	*Sorex*	*arcticus*	Rancholabrean
Canyon Basin Local Fauna	Assemblage	*Sorex*	*cinereus*	Pleistocene
Canyon City Club Cave	Cultural unit	Soricidae	unid	Post-Rancholabrean
Carrol Creek	Assemblage	*Sorex*	*arcticus*	Rancholabrean
Cave Without A Name	Assemblage	*Blarina*	*carolinensis*	Rancholabrean
Cave Without A Name	Assemblage	*Cryptotis*	*parva*	Rancholabrean
Cave Without A Name	Assemblage	*Notiosorex*	*crawfordi*	Rancholabrean
Cave Without A Name	Assemblage	*Sorex*	*cinereus*	Rancholabrean
Clear Creek Local Fauna	Assemblage	*Blarina*	sp.	Rancholabrean
Clear Creek Local Fauna	Assemblage	*Sorex*	*cinereus*	Rancholabrean
Deadman's Creek Local Fauna	Assemblage	*Blarina*	*brevicauda*	Irvingtonian
Deadman's Creek Local Fauna	Assemblage	*Sorex*	*cinereus*	Irvingtonian
Deadman's Creek Local Fauna	Assemblage	*Sorex*	*cudahyensis*	Irvingtonian
Deadman's Creek Local Fauna	Assemblage	*Sorex*	*lacustris*	Irvingtonian
Deadman's Creek Local Fauna	Assemblage	*Sorex*	*megapalustris*	Irvingtonian
Deadman's Creek Local Fauna	Assemblage	*Sorex*	*pratensis*	Irvingtonian
Deadman's Creek Local Fauna	Assemblage	*Sorex*	sp.	Irvingtonian

Site Name	Excavation Unit	Genus	Species	Age of Fauna
Dust Cave	Assemblage	*Cryptotis*	*parva*	Rancholabrean
Dust Cave	Assemblage	*Notiosorex*	*crawfordi*	Rancholabrean
Dust Cave	Assemblage	*Sorex*	*cinereus*	Rancholabrean
Dye Creek	Assemblage	*Cryptotis*	*parva*	Post-Rancholabrean
Easley Ranch Local Fauna	Quarry by the Bridge	*Blarina*	*brevicauda*	Pleistocene
Easley Ranch Local Fauna	Quarry by the Bridge	*Cryptotis*	*parva*	Pleistocene
Felton Cave	Assemblage	*Blarina*	*carolinensis*	Post-Rancholabrean
Felton Cave	Assemblage	*Cryptotis*	*parva*	Post-Rancholabrean
Felton Cave	Assemblage	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Fowlkes Cave	Late Pleistocene Deposit	*Notiosorex*	*crawfordi*	Rancholabrean
Fowlkes Cave	Late Pleistocene Deposit	*Sorex*	*palustris*	Rancholabrean
Fowlkes Cave	Late Pleistocene Deposit	*Sorex*	*vagrans*	Rancholabrean
Fowlkes Cave	Early-Recent Deposit	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Friesenhahn Cave	Unit 3B	*Blarina*	*carolinensis*	Rancholabrean
Friesenhahn Cave	Unit 3B	*Cryptotis*	*parva*	Rancholabrean
Friesenhahn Cave	Unit 2B and 2A	*Cryptotis*	*parva*	Holocene/Pleistocene
Friesenhahn Cave	Unit 2B and 2A	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Friesenhahn Cave	Unit 2C	*Blarina*	*carolinensis*	Holocene/Pleistocene
Friesenhahn Cave	Unit 2C	*Cryptotis*	*parva*	Holocene/Pleistocene
Friesenhahn Cave	Unit 2C	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Friesenhahn Cave	Unit 2D	*Blarina*	*carolinensis*	Holocene/Pleistocene
Friesenhahn Cave	Unit 2D	*Cryptotis*	*parva*	Holocene/Pleistocene
Friesenhahn Cave	Unit 2F	*Cryptotis*	*parva*	Holocene/Pleistocene
Friesenhahn Cave	Unit 3C	*Cryptotis*	*parva*	Holocene/Pleistocene
Friesenhahn Cave	Unit 3C	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Friesenhahn Cave	Unit 3D	*Cryptotis*	*parva*	Holocene/Pleistocene
Hall's Cave	150-155	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	150-155	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	150-155	*Notiosorex*	*crawfordi*	Rancholabrean
Hall's Cave	155-160	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	155-160	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	155-160	*Notiosorex*	*crawfordi*	Rancholabrean
Hall's Cave	160-165	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	160-165	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	160-165	*Notiosorex*	*crawfordi*	Rancholabrean
Hall's Cave	165-170	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	165-170	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	170-175	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	170-175	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	175-180	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	175-180	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	175-180	*Notiosorex*	*crawfordi*	Rancholabrean

Site Name	Excavation Unit	Genus	Species	Age of Fauna
Hall's Cave	180-185	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	185-190	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	185-190	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	185-190	*Notiosorex*	*crawfordi*	Rancholabrean
Hall's Cave	185-190	*Sorex*	sp.	Rancholabrean
Hall's Cave	190-195	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	190-195	*Notiosorex*	*crawfordi*	Rancholabrean
Hall's Cave	195-200	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	195-200	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	195-200	*Notiosorex*	*crawfordi*	Rancholabrean
Hall's Cave	200-205	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	200-205	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	205-210	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	205-210	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	210-215	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	210-215	*Cryptotis*	*parva*	Rancholabrean
Hall's Cave	215-220	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	215-220	*Sorex*	sp.	Rancholabrean
Hall's Cave	220-225	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	220-230	*Sorex*	sp.	Rancholabrean
Hall's Cave	225-230	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	230-235	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	230-235	*Notiosorex*	*crawfordi*	Rancholabrean
Hall's Cave	230-235	*Sorex*	sp.	Rancholabrean
Hall's Cave	235-240	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	235-240	*Sorex*	sp.	Rancholabrean
Hall's Cave	240-245	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	245-250	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	245-250	*Sorex*	sp.	Rancholabrean
Hall's Cave	250-255	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	255-260	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	255-260	*Sorex*	sp.	Rancholabrean
Hall's Cave	270-275	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	300-305	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	315-320	*Blarina*	*carolinensis*	Rancholabrean
Hall's Cave	145-150	*Blarina*	*carolinensis*	Holocene/Pleistocene
Hall's Cave	145-150	*Cryptotis*	*parva*	Holocene/Pleistocene
Hall's Cave	145-150	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Hall's Cave	0-5	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	100-105	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	100-105	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	100-105	*Blarina*	*carolinensis*	Post-Rancholabrean
Hall's Cave	100-105	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	100-105	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	105-110	*Blarina*	*carolinensis*	Post-Rancholabrean
Hall's Cave	105-110	*Cryptotis*	*parva*	Post-Rancholabrean

Site Name	Excavation Unit	Genus	Species	Age of Fauna
Hall's Cave	105-110	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	105-120	*Blarina*	*carolinensis*	Post-Rancholabrean
Hall's Cave	110-115	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	110-115	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	115-120	*Blarina*	*carolinensis*	Post-Rancholabrean
Hall's Cave	115-120	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	115-120	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	120-125	*Blarina*	*carolinensis*	Post-Rancholabrean
Hall's Cave	120-125	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	120-125	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	125-130	*Blarina*	*carolinensis*	Post-Rancholabrean
Hall's Cave	125-130	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	125-130	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	130-135	*Blarina*	*carolinensis*	Post-Rancholabrean
Hall's Cave	130-135	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	130-135	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	135-140	*Blarina*	*carolinensis*	Post-Rancholabrean
Hall's Cave	135-140	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	135-140	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	140-145	*Blarina*	*carolinensis*	Post-Rancholabrean
Hall's Cave	140-145	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	140-145	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	15-20	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	20-25	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	20-25	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	25-30	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	25-30	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	30-35	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	30-35	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	35-40	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	35-40	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	40-45	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	45-50	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	50-55	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	50-55	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	50-55	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	50-55	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	55-60	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	55-60	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	60-65	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	60-65	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	65-70	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	65-70	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	70-75	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	70-75	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	75-80	*Cryptotis*	*parva*	Post-Rancholabrean

Site Name	Excavation Unit	Genus	Species	Age of Fauna
Hall's Cave	75-80	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	80-85	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	80-85	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	85-90	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	85-90	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	90-95	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	90-95	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Hall's Cave	95-100	*Cryptotis*	*parva*	Post-Rancholabrean
Hall's Cave	95-100	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Howard Ranch	Assemblage	*Blarina*	*brevicauda*	Rancholabrean
Howard Ranch	Assemblage	*Cryptotis*	*parva*	Rancholabrean
Howard Ranch	Assemblage	*Sorex*	*cinereus*	Rancholabrean
Howard Ranch	Assemblage	*Sorex*	*palustris*	Rancholabrean
Kitchen Door	Assemblage	*Cryptotis*	*parva*	Irvingtonian
Kyle	Stratum 2	*Cryptotis*	*parva*	Post-Rancholabrean
Kyle	Stratum 3	*Cryptotis*	*parva*	Post-Rancholabrean
Laubach Cave No. 2	Assemblage	*Cryptotis*	*parva*	Rancholabrean
Laubach Cave No. 4	Assemblage	*Blarina*	*carolinensis*	Rancholabrean
Laubach Cave No. 4	Assemblage	*Cryptotis*	*parva*	Rancholabrean
Lewisville 1978-1980	Assemblage	*Cryptotis*	*parva*	Rancholabrean
Longhorn Cavern	Red Fill	*Blarina*	*carolinensis*	Rancholabrean
Longhorn Cavern	Red Fill	*Cryptotis*	*parva*	Rancholabrean
Longhorn Cavern	Black Fill	*Cryptotis*	*parva*	Post-Rancholabrean
Longhorn Cavern	Black Fill	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Lower Sloth Cave	Trench 1	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Lower Sloth Cave	Trench 2	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Lower Sloth Cave	Trench 3	*Cryptotis*	*parva*	Holocene/Pleistocene
Lower Sloth Cave	Trench 5	*Cryptotis*	*parva*	Holocene/Pleistocene
Lower Sloth Cave	Trench 5	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Lower Sloth Cave	Trench 5	*Sorex*	*cinereus*	Holocene/Pleistocene
Lower Sloth Cave	Trench 5	*Sorex*	*vagrans*	Holocene/Pleistocene
Lower Sloth Cave	Trench 6	*Cryptotis*	*parva*	Holocene/Pleistocene
Lower Sloth Cave	Trench 6	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Lower Sloth Cave	Trench 6	*Sorex*	*vagrans*	Holocene/Pleistocene
Lubbock Lake	Stratum IB	*Blarina*	*sp.*	Rancholabrean
Lubbock Lake	Stratum 2ALB2-3	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Lubbock Lake	Stratum 2B cienega	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Mayfield Ranch Local Fauna	Assemblage	*Sorex*	*cinereus*	Irvingtonian
Miller's Cave	Travertine	*Blarina*	*brevicauda*	Post-Rancholabrean
Miller's Cave	Travertine	*Cryptotis*	*parva*	Post-Rancholabrean
Moore Pit	Assemblage	*Cryptotis*	*parva*	Rancholabrean
Patterson Ranch Local Fauna	Assemblage	*Cryptotis*	*parva*	Pleistocene
Patterson Ranch Local Fauna	Assemblage	*Sorex*	sp.	Pleistocene

Site Name	Excavation Unit	Genus	Species	Age of Fauna
Pratt Cave	Assemblage	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Rattlesnake Cave	Zone 1	*Cryptotis*	*parva*	Post-Rancholabrean
Rattlesnake Cave	Zone 1	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Rattlesnake Cave	Zone 2	*Cryptotis*	*parva*	Post-Rancholabrean
Rattlesnake Cave	Zone 2	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Rattlesnake Cave	Zone 3	*Cryptotis*	*parva*	Post-Rancholabrean
Rattlesnake Cave	Zone 3	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Rattlesnake Cave	Zone 4	*Cryptotis*	*parva*	Post-Rancholabrean
Rattlesnake Cave	Zone 4	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Rex Rodgers	Assemblage	*Blarina*	*sp.*	Post-Rancholabrean
Schulze Cave	Layer C2	*Blarina*	*brevicauda*	Holocene/Pleistocene
Schulze Cave	Layer C2	*Cryptotis*	*parva*	Holocene/Pleistocene
Schulze Cave	Layer C2	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Schulze Cave	Layer C2	*Sorex*	*cinereus*	Holocene/Pleistocene
Schulze Cave	Layer B	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Schulze Cave	Layer C1	*Blarina*	*brevicauda*	Post-Rancholabrean
Schulze Cave	Layer C1	*Cryptotis*	*parva*	Post-Rancholabrean
Schulze Cave	Layer C1	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Schulze Cave	Layer C1	*Sorex*	*cinereus*	Post-Rancholabrean
Schulze Cave	Layer C1	*Sorex*	*vagrans*	Post-Rancholabrean
Seminole Sink	Deep Profile	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Seminole Sink	East Pit	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Seminole Sink	Zone 1	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Seminole Sink	Zone 2	*Notiosorex*	*crawfordi*	Post-Rancholabrean
Sims Bayou Local Fauna	South Bank across from Prison Farm	*Cryptotis*	*parva*	Pleistocene
Slaton Quarry Local Fauna	Yellow Canyon	*Sorex*	*vagrans*	Rancholabrean
Swan Lake	Assemblage			Post-Rancholabrean
Upper Sloth Cave	10-20 cm level	*Cryptotis*	*parva*	Rancholabrean
Upper Sloth Cave	10-20 cm level	*Notiosorex*	*crawfordi*	Rancholabrean
Upper Sloth Cave	10-20 cm level	*Sorex*	*cinereus*	Rancholabrean
Upper Sloth Cave	20-30 cm level	*Notiosorex*	*crawfordi*	Rancholabrean
Upper Sloth Cave	30-40 cm level	*Notiosorex*	*crawfordi*	Rancholabrean
Upper Sloth Cave	0-10 cm level	*Notiosorex*	*crawfordi*	Holocene/Pleistocene
Vera Local Faunule	Assemblage	*Blarina*	*brevicauda*	Irvingtonian
Vera Local Faunule	Assemblage	*Cryptotis*	*parva*	Irvingtonian
Vera Local Faunule	Assemblage	*Sorex*	*cinereus*	Irvingtonian
Wilson-Leonard	Assemblage	*Blarina*	sp.	Post-Rancholabrean
Wilson-Leonard	Assemblage	*Cryptotis*	*parva*	Post-Rancholabrean
Zesch Cave	Assemblage	*Blarina*	*carolinensis*	Rancholabrean
Zesch Cave	Assemblage	*Cryptotis*	*parva*	Rancholabrean
Zesch Cave	Assemblage	*Notiosorex*	*crawfordi*	Rancholabrean
Zesch Cave	Assemblage	*Sorex*	*hoyi*	Rancholabrean

The distribution of Quaternary sites that contain fossil *Notiosorex* falls entirely within the modern distribution of *Notiosorex crawfordi* (Figure 4.12). I have presented both the distributional areas for extant shrews (Patterson et al., 2007) and the locations of vouchered museum specimens (MaNIS). All collections that are part of the MaNIS system were queried for shrew specimens from Texas. A list of all collections is found in Appendix D. There are biases associated with visualizing both point and shaded area data. Shaded distribution maps tend to overestimate the range of taxa (LaDuc and Bell, 2010). The point data from MaNIS are incomplete because only the records that have geographic coordinates are shown. Many of the specimens listed in the MaNIS database are missing latitude and longitude data so they are not shown on the maps. If the shaded range maps overestimate the present range of shrews, then it is more significant if they were found outside of the shaded range in the past.

There is some overlap between the distribution of Quaternary sites that contain *Cryptotis* and the modern distribution of *Cryptotis parva* (Figure 4.13). There is an eastward range contraction of *Cryptotis* from the Holocene to the present. This includes two Post-Rancholabrean age sites that are outside of the modern range. Specimens were identified as *Cryptotis parva* and no other species of *Cryptotis* were reported.

All reported Quaternary records of *Blarina* are outside of the modern range of both species of *Blarina* that occur in Texas today (Figure 4.14). Several sites were reported to have *Blarina brevicauda*. Though present in Texas today, there are no reported records of *Blarina hylophaga*.

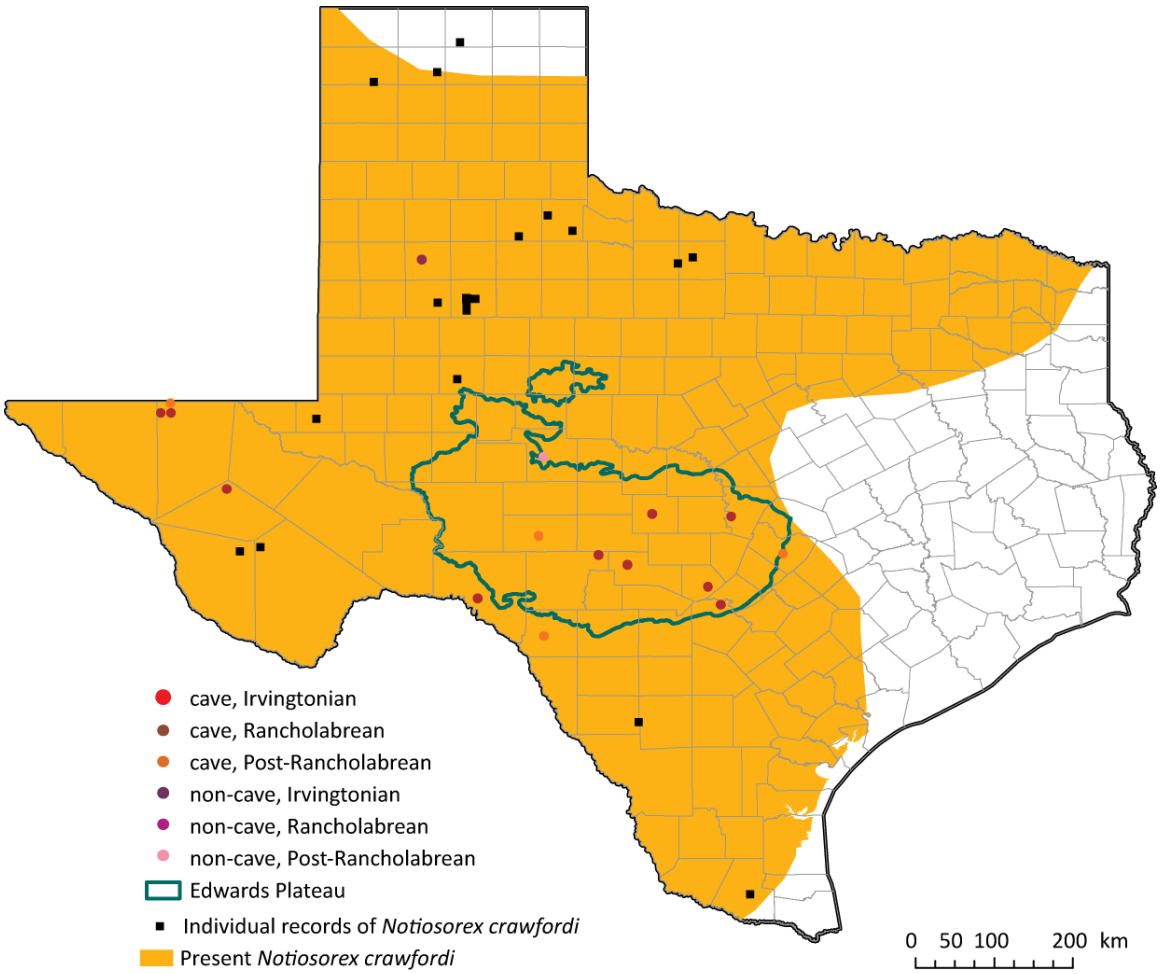


Figure 4.12. Quaternary sites with *Notiosorex* are round symbols. The black square symbols show collection records from MaNIS database of extant *Notiosorex crawfordi*.

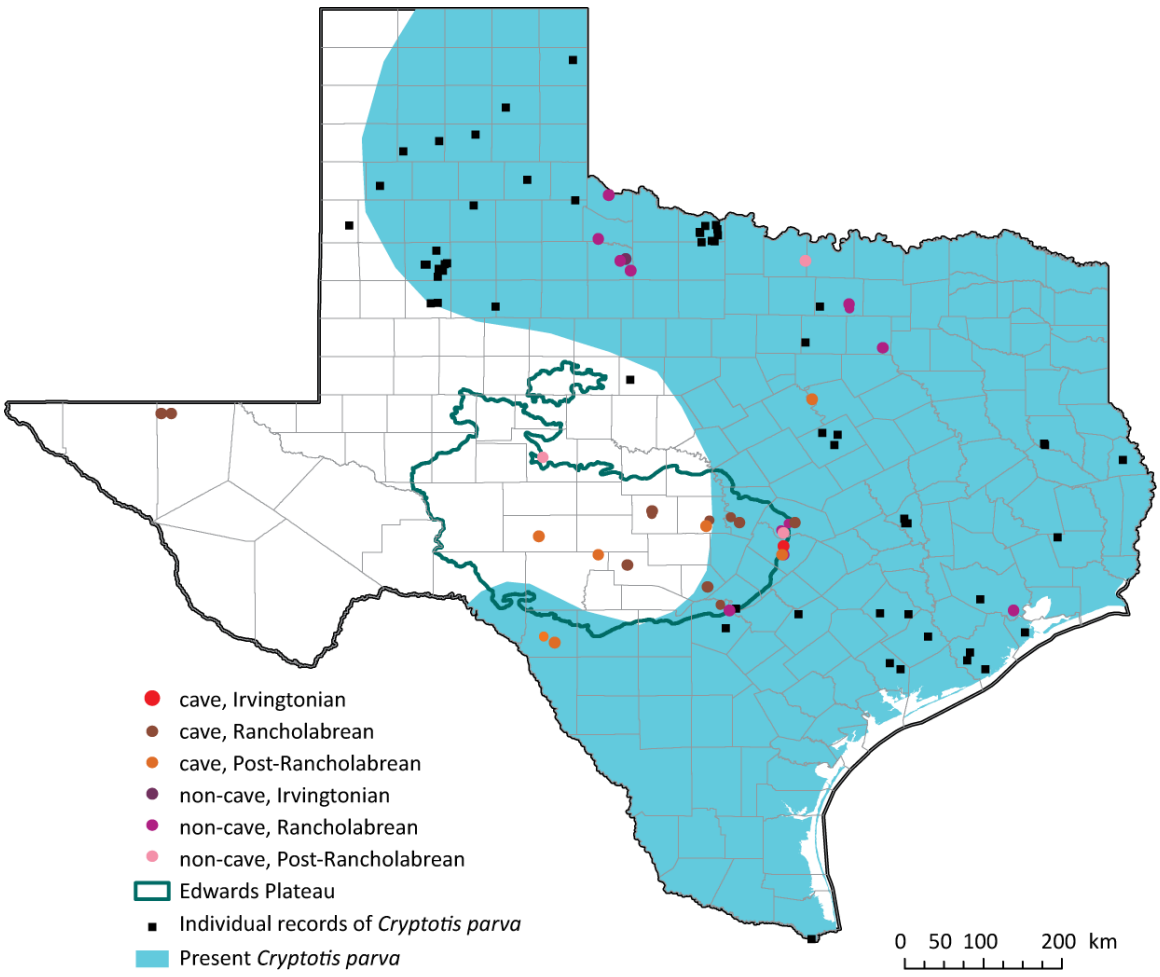


Figure 4.13. Quaternary sites with *Cryptotis* are round symbols. The black square symbols show collection records from MaNIS database of extant *Cryptotis parva*.

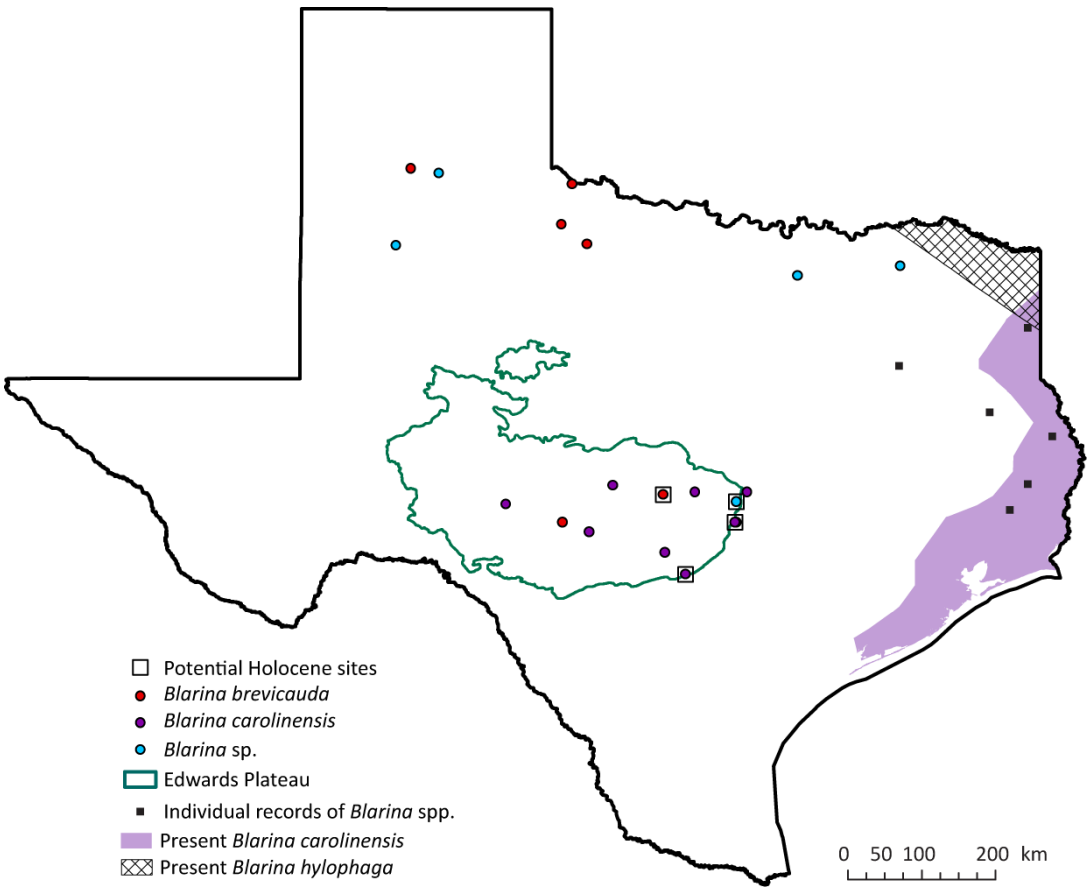


Figure 4.14. Quaternary sites with *Blarina* are round symbols. The black square symbols show collection records from MaNIS database of extant *Blarina* spp.

No species of *Sorex* are found within Texas today. However, several extant species occur in close proximity to Texas. *Sorex* was reported in the FAUNMAP II database from 20 Quaternary sites, as ten different species of *Sorex*, as well as, unidentified specimens of *Sorex* (Figure 4.15). Some of the species reported from the Pleistocene are extinct; the extant species are from varying distances outside of Texas.

I generated GIS maps that show the extant range of a number of species of mammals and the Quaternary sites that have fossils identified as the same species. I produced a map and distributional ellipses for *Odocoileus hemionus* and *Odocoileus virginianus*, and for *Spilogale gracilis* and *Spilogale putorius*. I also produced range maps for *Chaetodipus hispidus, Chaetodipus intermedius, Chaetodipus nelsoni, Dipodomys elator, Dipodomys merriami, Dipodomys ordii, Dipodomys spectabilis, Perognathus flavus,* and *Perognathus merriami*.

DISCUSSION

Site distribution

Unsurprisingly, there are strong geographic influences on site location. The distribution of cave versus non-cave sites is not random (Figure 4.2), and many factors account for the distribution of Quaternary sites (Figures 4.3, 4.4, 4.5, 4.6, and 4.7). Most of the caves in Texas are found on the Edwards Plateau (Figure 4.5). That area contains many karst features, including sinkholes, caves, and springs, and is covered by little soil. Although non-cave Quaternary sites show a broad distribution across all of Texas, they are most common in east and north Texas where there are large accumulations of sediments (e.g., terrace deposits). Both cave and non-cave sites in Texas are common along current or past rivers and streams indicating a close relationship with local surface

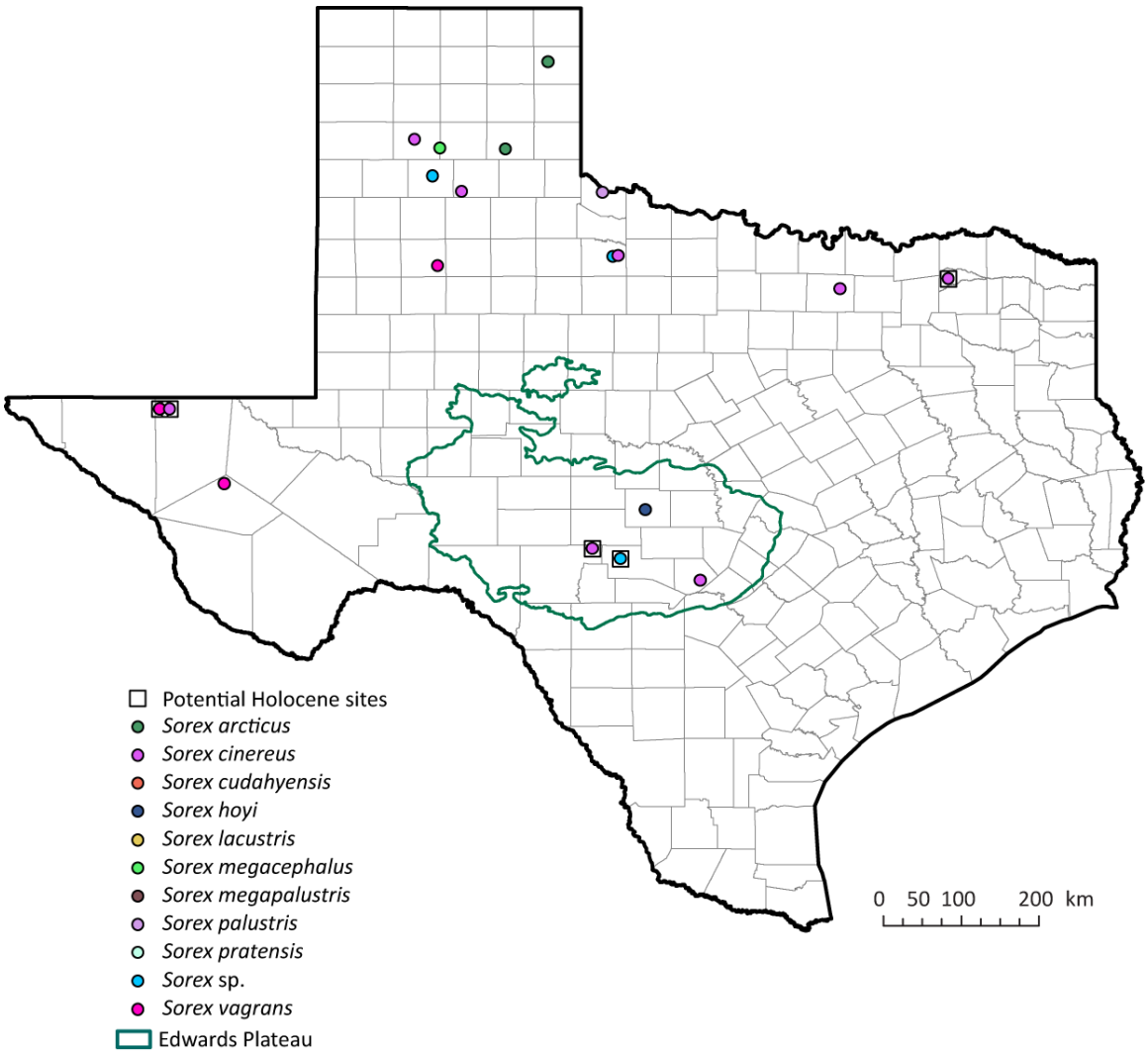


Figure 4.15. Quaternary sites that have specimens identified as species of *Sorex*. No extant S*orex* are found within Texas.

hydrology. This may be because streams and rivers are among the few areas with public access to land in Texas (Figure 4.5). Most of the land is privately owned in Texas and this makes access to sites difficult.

Given the differences between the geographic distributions of cave and non-cave sites, there are potential problems if paleoecologic interpretations are made without considering geography. The diversity of taxa preserved in cave faunas is incredibly valuable for paleoecologic reconstructions, but the older (Rancholabrean) sites are restricted to central Texas. The non-cave sites are found across Texas, but more than half of those sites preserve only one taxon and so provide little paleoecologic information.

Geographic bias in the identification of fossils

GIS provides a powerful tool for analyzing the paleoecology of Quaternary mammals. First, the maps generated by GIS quickly convey the differences between the modern distributions of species and the distributions in the Quaternary. All subsequent interpretations begin with the identification of fossils. The shrews from Quaternary sites were identified with both morphological characteristics and geographic or temporal assumption (Chapter 2). This affects the interpretations that can be made from the fossils.

Before 2000, the genus *Notiosorex* included a single extant species, *Notiosorex crawfordi* (Carraway and Timm, 2000). There was an extinct species from the Pliocene of Kansas named by Claude Hibbard, *Notiosorex jacksoni* (Hibbard, 1950). The diagnosis of this species was that it was larger than *Notiosorex crawfordi* and smaller then *Megasorex gigas*. All Quaternary fossils of *Notiosorex* are identified as *Notiosorex crawfordi* in the FAUNMAP II database (Graham and Lundelius, 2010). Recently several more species of

Notiosorex were named as distinct species in both extant and extinct contexts in southwestern North America, bringing the number of recognized species of *Notiosorex* to eight (Carraway and Timm, 2000; Carraway, 2010), and calling into question most earlier published species identifications of fossils. Further confusing the issue is the lack of morphological features distinguishing two of the extant species, *Notiosorex cockrumi* and *Notiosorex crawfordi*, which can only be differentiated by genetic data (Baker, O'Neill, and McAliley, 2003).

All of the specimens of *Cryptotis* in the FAUNMAP II database were identified as *Cryptotis parva* (Graham and Lundelius, 2010). There are at least 30 named extant species of *Cryptotis* (Hutterer, 2005), but only *Cryptotis parva* is found in the United States. All of the specimens in the FAUNMAP II database are identified to species; there are no specimens identified as *Cryptotis* sp. There are apomorphies that can separate *Cryptotis parva* from other species of *Cryptotis* (Chapter 2), however these were not used to identify any of the specimens in the database. Therefore, the only conclusion that can be reached is that the comparison pool of species used to identify *Cryptotis* only included *Cryptotis parva*. This is a clear case of geographic bias in the identification. The FAUNMAP II database includes Mexico, where a number of other species of *Cryptotis* are found, yet they have not been recognized in the fossil record.

The recognition of species of *Blarina* has a more complex history. *Blarina* is found only in the eastern United States and Canada. Three currently recognized species of *Blarina* are *Blarina brevicauda*, *Blarina carolinensis*, and *Blarina hylophaga*. Recently, *Blarina shermani* was elevated from a subspecies of *Blarina carolinensis* based on its larger size relative to *Blarina carolinensis* (Benedict et al., 2006). *Blarina shermani* is found only in a geographically restricted area of Florida near Fort Myers. The species of *Blarina* are nearly impossible to discriminate from each other with only craniodental

characters. Few morphological characters can be used to identify species (Chapter 2). Size and geographic range were suggested previously to separate species, but there is overlap in both. It was suggested that the most reliable way to differentiate extant species is by karyotype (Thompson et al. 2011). However, no genetic material for *Blarina shermani* has been collected (Benedict et al., 2006), and genetic material is generally unavailable for fossils.

Within the FAUNMAP II database, the fossils of *Blarina* from Texas were identified as *Blarina brevicauda*, *Blarina carolinensis*, and *Blarina* sp. Specimens from the Easley Ranch Local Fauna and the Vera Local Faunule were reported in FAUNMAP II as *Blarina* cf. *brevicauda* (Graham and Lundelius, 2010). Two extant species are found in Texas today, *Blarina carolinensis* and *Blarina hylophaga*. The species names of *Blarina* in the FAUNMAP II database are biased by the time when they were identified, and by geography. *Blarina brevicauda* was the first species named. It was not until 1972 that a second species, *Blarina carolinensis*, was widely accepted (Genoways and Choate, 1972). One other species, *Blarina telmalestes*, was dubiously accepted at the time (Genoways and Choate, 1972). Quaternary fossils of *Blarina* identified prior to 1972 were all assumed to belong to *Blarina brevicauda*. An extinct Irvingtonian species, *Blarina ozarkensis* was named in 1976 (Graham and Semken, 1976). In 1981, another subspecies, *Blarina hylophaga*, was elevated to species status, (George et al., 1981). *Blarina hylophaga* was recognized as distinct based on karyotype, and the only widely accepted morphological characteristic used to separate *Blarina hylophaga* from *Blarina carolinensis* is the angle of the first lower incisor to the dentary [>18° for *Blarina hylophaga* and <17° for *Blarina carolinensis* (Carraway, 1995)]. However, I found this character to be nearly useless for differentiating those species (Chapter 2).

The size of specimens and some geographic assumptions led to fossils being identified as *Blarina carolinensis* in Texas subsequent to the recognition of that species. I found no justification for why those specimens could not be identified as *Blarina hylophaga* (e.g., Toomey, 1993; Sagebiel, 2010), because the extant ranges of both species are approximately equally distant from most fossil localities in Texas. It is not just within Texas that *Blarina hylophaga* is generally unrecognized in the fossil record. Only two localities in the FAUNMAP II database are reported to contain *Blarina hylophaga*: Peccary Cave, AR and Doby Springs Local Fauna, OK. However, in both cases the fossils were originally identified as *Blarina brevicauda*. I could not find a published revision of the identification, so this may be an error in the FAUNMAP II database.

Given the numerous potential problems with the identification of species of shrews, I suggest there may be additional problems with the identification of other species of mammals as listed in the FAUNMAP II database. GIS can be used to identify species that may have been identified with geographic assumptions. I found potential identification problems within several different orders of mammals using GIS.

Differentiating species of *Odocoileus* based on skeletal morphology alone is a challenge (Ayer, 1936). Antlers shape differs between *Odocoileus virginianus* and *Odocoileus hemionus*. However, sympatric populations of *Odocoileus virginianus* and *Odocoileus hemionus* in western Texas can interbreed and produce hybrid offspring that are more characteristic of *Odocoileus virginianus*, further complicating identification (Schmidly, 2004). Figure 4.16 shows the Quaternary sites in Texas reported to contain *Odocoileus*. There are three localities with *Odocoileus hemionus*, Alibates, Ceremonial Cave, and Williams Cave. Williams Cave is the only site reported to contain both *Odocoileus hemionus* and *Odocoileus virginianus*. There are morphological characteristics provided for the identification of those species at Williams Cave (Ayer, 1936). *Odocoileus*

virginianus is the more common of the two species in the modern fauna of Texas, and this is true in the fossil record of Texas, also. There is a strong prejudice towards the identification of fossils of *Odocoileus* being identified to species in the same area where

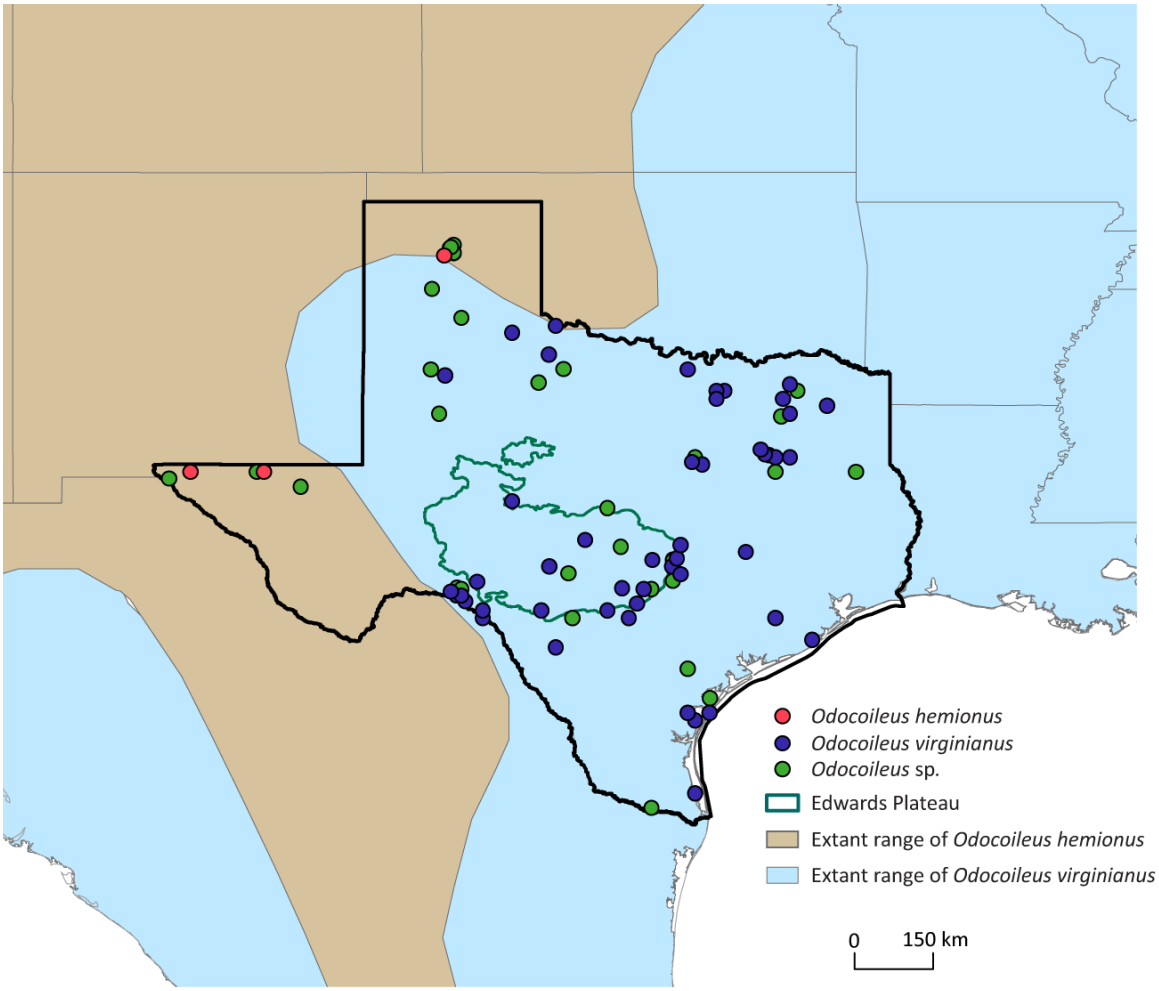


Figure 4.16. Quaternary sites queried from the FAUNMAP II that have identified specimens of *Odocoileus*.

the modern species live (Figure 4.17). No specimens of *Odocoileus hemionus* were identified outside of its modern range in Texas. This is strongly suggestive that some level of geographic bias was used to identify species of *Odocoileus*. Though it is possible that there was little to no range shift for those species since the Pleistocene, this warrants further investigation to determine whether some specimens of *Odocoileus virginianus* were misidentified. If it is not possible to differentiate these two species based on skeletal material then the specimens should be identified as *Odocoileus* sp.

There are potential geographic biases associated with the identification of fossil skunks as well. *Spilogale gracilis*, the western spotted skunk, was identified only from west Texas, entirely within the modern range of the species. The species *Spilogale putorius*, eastern spotted skunk, was identified from sites farther west than the present range (Figure 4.18). There is a substantial difference in the shape and position of the standard deviational ellipses for these species indicating there is a difference in the location of fossils of the different species (Figure 4.19). This could indicate a geographic bias in the identifications; however, it does not indicate whether the bias is due to the actual difference in the species ranges, or whether geography was used to identify the species.

Heteromyid rodents (pocket mice and kangaroo rats) are common in Quaternary faunas of Texas. Though readily differentiable from other rodents, it can be difficult to distinguish species and even genera from one another (Paulson, 1988; Best and Skupski, 1994; Schmidly, 2004). There are three genera of heteromyids with multiple extant species in Texas, *Chaetodipus*, *Perognathus*, and *Dipodomys*. *Liomys irroratus* also occurs in Texas, but there are no Quaternary records of the genus in Texas. There are four species of *Chaetodipus* found in Texas today (Schmidly, 2004), and there are 16 named species (Wilson and Reeder, 2005). At all but two localities, the only species of

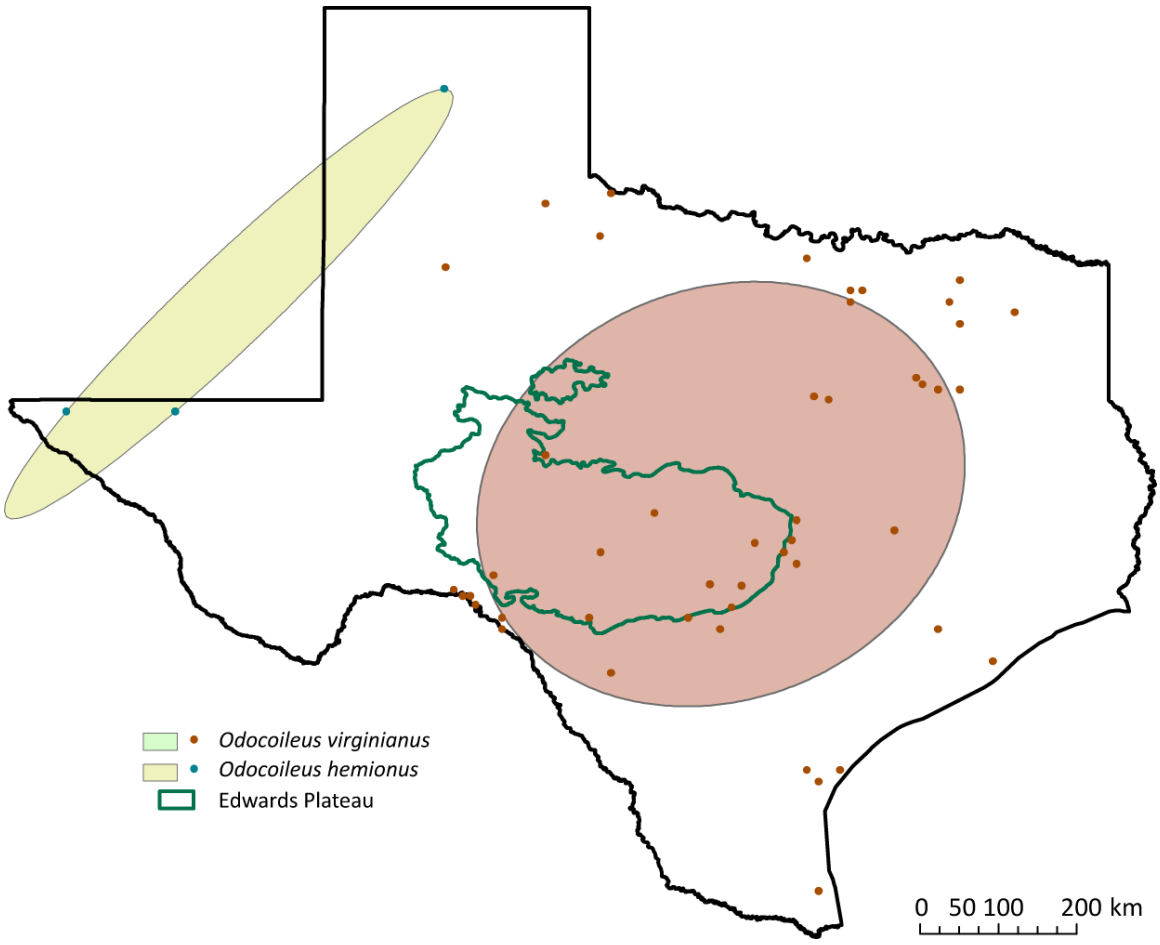


Figure 4.17. Standard deviation ellipses for *Odocoileus virginianus* and *Odocoileus hemionus*. The ellipses show the difference in non-overlapping areas between where the two species were identified from fossil sites.

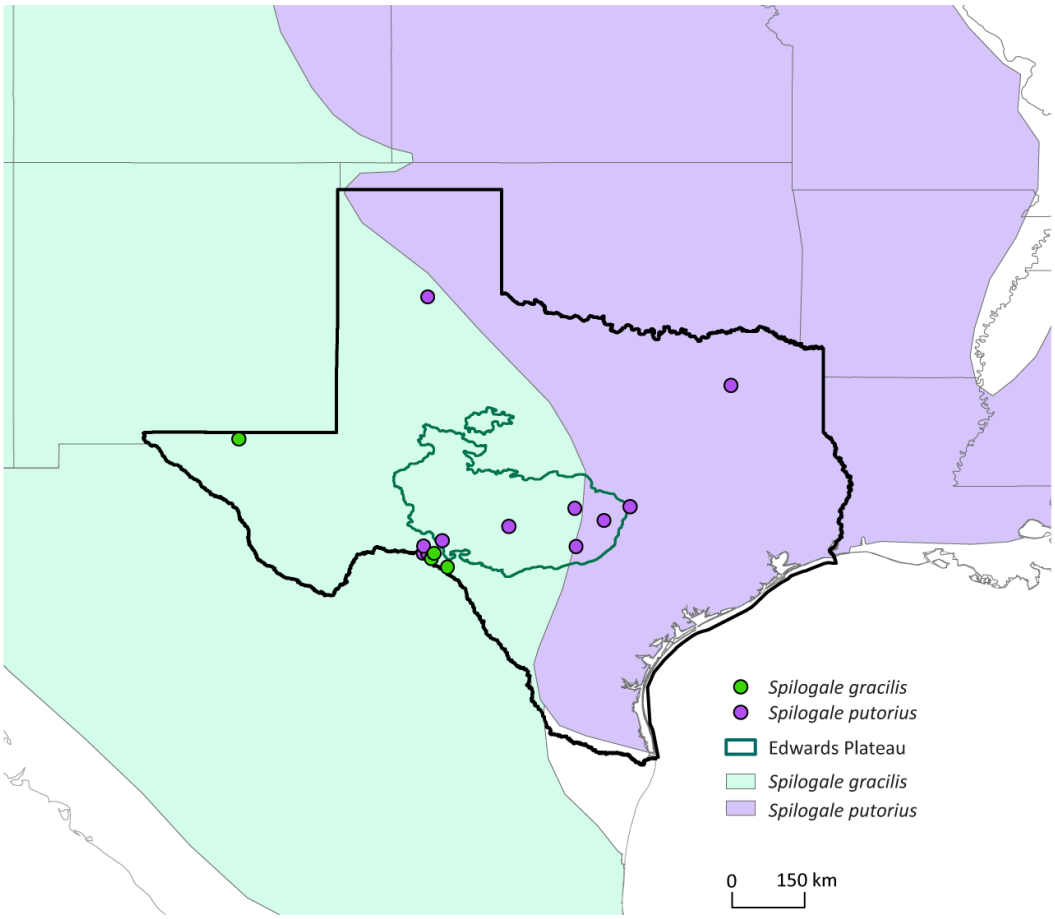


Figure 4.18. Quaternary sites queried from the FAUNMAP II that have identified specimens of *Spilogale*.

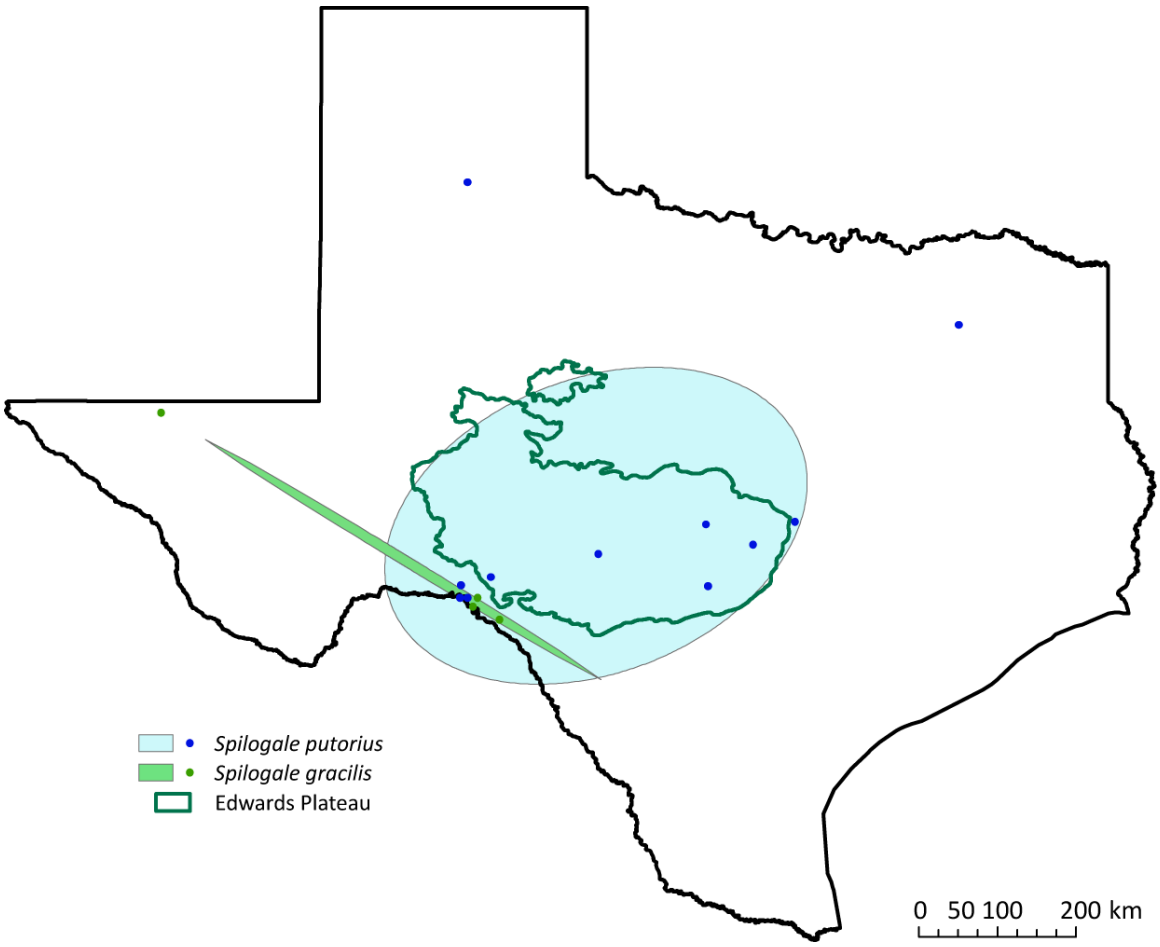


Figure 4.19. Standard deviation ellipses for *Spilogale gracilis* and *Spilogale putorius*. There is a significant difference between the areas where the two species were identified from fossil sites.

Chaetodipus identified was *Chaetodipus hispidus*. In addition to *Chaetodipus hispidus*, *Chaetodipus intermedius* was identified at Williams Cave and *Chaetodipus nelsoni* was identified at Seminole sink (Graham and Lundelius, 2010). The original identification at Williams Cave was *Perognathus* (*Chaetodipus*) *intermedius* (Ayer, 1936). The subgenus *Chaetodipus* was not elevated to genus until 1983 (Hafner and Hafner, 1983). Therefore, the taxonomy has been updated in the FAUNMAP II database.

The four species of *Chaetodipus* are sympatric for part of their range in Texas. *Chaetodipus intermedius* and *Chaetodipus nelsoni* were only identified as fossils where they are presently found in Texas (Figure 4.20). *Chaetodipus hispidus* has the largest range of a species of *Chaetodipus* in Texas today and this corresponds with the identification of fossils. It is noteworthy that *Chaetodipus hispidus* is one of the most commonly identified fossils in Quaternary faunas from central Texas. It is represented by at least 2390 cataloged specimens from Hall's Cave and 1300 and 743 specimens at Friesenhahn Cave and Schulze Cave, respectively (Toomey, 1993). However, the only characteristic used to distinguish species was size (Toomey, 1993). Given the change in taxonomy of this genus in 1983, many of the fossils were identified before then, and that the identified fossils have a strong correspondence of to geography, it suggests that the identifications of these fossils should be re-examined.

Dipodomys is a speciose genus of heteromyid. 18 extant species of *Dipodomys* are recognized (Wilson and Reeder, 2005). There are four species of *Dipodomys* identified from fossil sites in Texas, *Dipodomys elator*, *Dipodomys merriami*, *Dipodomys ordii*, and *Dipodomys spectabilis*. However, more sites have specimens identified as *Dipodomys* sp. than as individual species. Three species (*Dipodomys merriami*, *Dipodomys ordii*, and *Dipodomys spectabilis*) were identified at Fowlkes Cave and two species (*Dipodomys ordii*

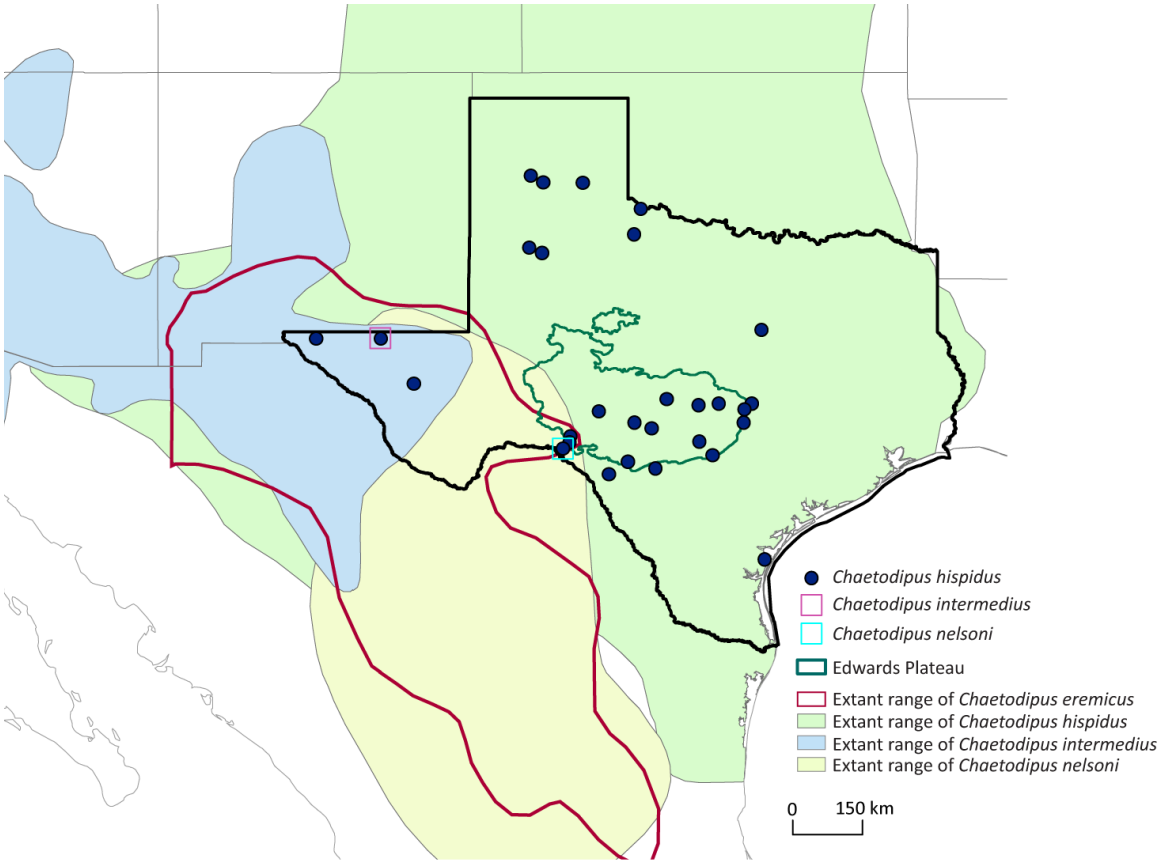


Figure 4.20. Quaternary sites from FAUNMAP II that have identified specimens of *Chaetodipus* are shown as point data. Note the close correspondence with the overlapping modern ranges of species of *Chaetodipus*.

and *Dipodomys spectabilis*) were identified at Hueco Tanks State Historic Park and Pratt Cave (Figure 2.21). It is notable that multiple species were identified, but they correspond closely to the modern ranges of those species. *Dipodomys elator* was identified outside of its modern range, but neither *Dipodomys compactus* nor *Dipodomys nelsoni* whose modern ranges are near or within Texas are recognized from fossils.

There are three species of *Perognathus* found in Texas today, *Perognathus flavescens*, *Perognathus flavus*, and *Perognathus merriami* (Schmidly, 2004). However, only two of these species, *Perognathus flavus* and *Perognathus merriami*, were identified as fossils in the FAUNMAP II database (Graham and Lundelius, 2010). None of the fossil sites where those species were identified is within the modern range of *Perognathus flavescens* or *Perognathus flavus* but only *Perognathus flavus* was identified (Figure 4.22). The majority of *Perognathus* fossil specimens are not identified to species. *Perognathus flavus* is most similar to *Perognathus merriami*, and the two can hybridize (Best and Skupski, 1994). As is pointed out by Best and Skupski (1994) for extant specimens, "No single set of characters will distinguish all *P. flavus* from all *P. merriami*" (Best and Skupski, 1994, p. 1). I question the validity of the species identifications of Quaternary fossils of this taxon. Clearly there are extreme challenges to differentiating those species with fragmentary fossil material. This would suggest that taxonomic identifications above the species level would be more valid.

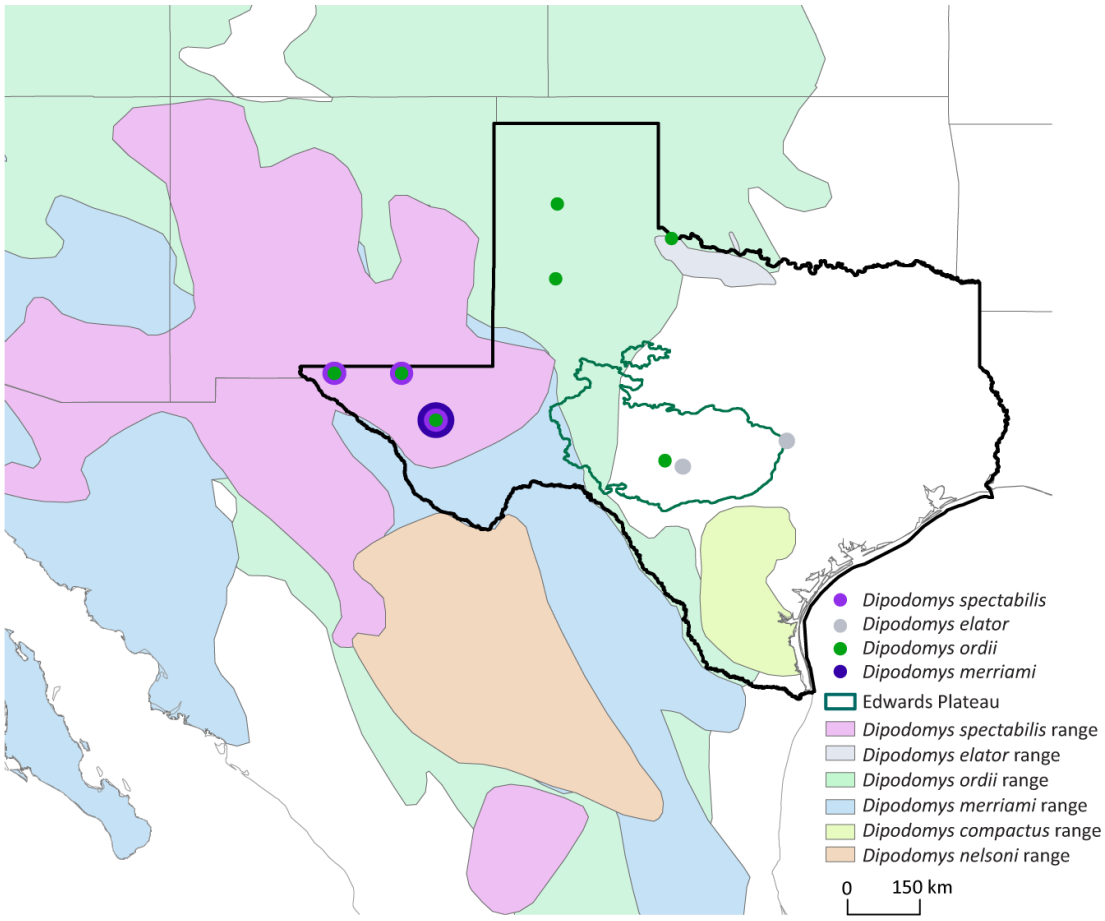


Figure 4.21. Quaternary sites queried from the FAUNMAP II that have identified specimens of *Dipodomys* shown with the modern overlapping ranges of species of *Dipodomys*. Note that there are six modern species with ranges in or near Texas, yet only four species were identified from fossils.

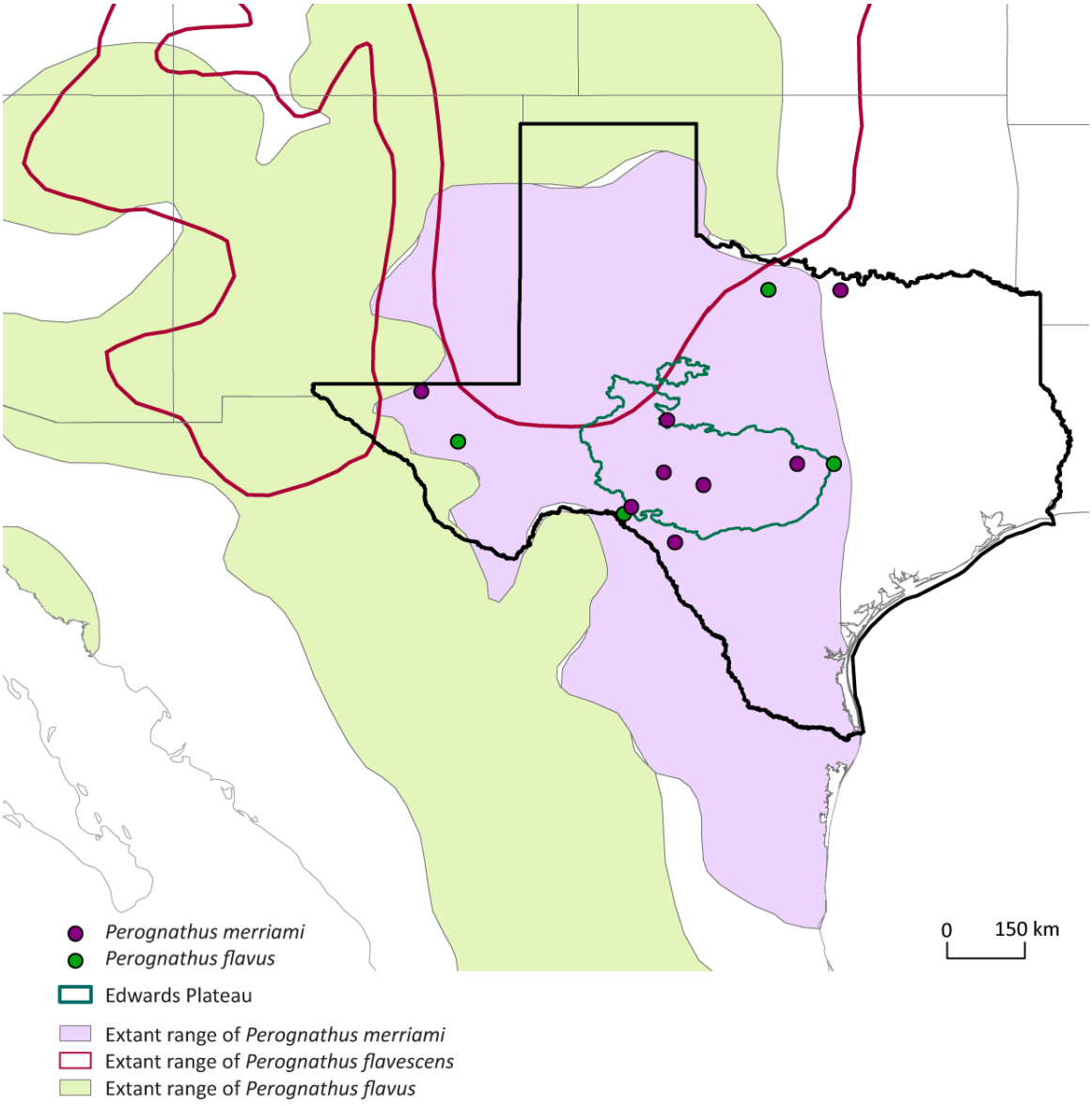


Figure 4.22. Quaternary sites from the FAUNMAP II with identified specimens of *Perognathus* shown as point data. They are shown here with the modern ranges of species of *Perognathus*.

Utility of higher-level taxonomic groups

In general, it is more likely that higher taxonomic groups (e.g., Soricidae) will be more accurately identified. There should be equal or higher confidence that a fossil is correctly identified as a mammal, than the confidence that it is identified as a particular species of mammal. In all cases, the taxonomic name in the database is dependent on how the original specimen was identified. However, it is likely that, at least for shrews, the genera are probably more accurately identified than species because there are a number of reliable characteristics that can be used to differentiate the genera (Chapter 2). In effect, most workers were identifying genera and using geography to add the species epithet. Most workers were using geographic assumptions, whether explicitly or not, to refine species identifications, and were, in effect, making generic identifications. For taxa like *Notiosorex* and *Blarina*, for which there was only a single species recognized for most of the twentieth century, those identifications should be treated as generic identifications until they are reevaluated against the full diversity of species. Because there is much uncertainty in the identification of fossil shrew species, I tested whether valuable paleoecologic information could be gained from taxonomic units above the species level. Therefore, I restricted my paleoecologic analysis of shrews to the generic level.

The independent paleoclimate proxies for central Texas include pollen, C^{13} isotopes, magnetic susceptibility, speleothem, and sedimentation records (Nordt et al., 1994; Musgrove et al. 2001; Cooke, 2005; Elwood and Gose, 2006; Boulter et al., 2010). On average the climate on the Edwards Plateau went from cool and wet in the latest Pleistocene to warm and dry at present. All paleoclimate proxy evidence suggests that from 12 to 15 ka it was much wetter and cooler on the Edwards Plateau. Around 12 ka the warming and drying trend began and by 8 to 10 ka conditions were similar to today. The C^{13} isotopes, magnetic susceptibility, and pollen records are detailed enough to show

that much of the Holocene was even drier than today, but with short humid periods (Nordt et al., 1994; Elwood and Gose, 2006; Boulter et al., 2010). These proxies indicate that maximum dry conditions occurred around 5 ka. Around 2 ka conditions were wetter and cooler than today and current conditions began less than 2 ka.

The environmental conditions during Late Pleistocene were significantly cooler and wetter across central Texas than conditions during the Holocene. Therefore, taxa that are presently adapted to cool and wet conditions could have had geographically larger ranges during the Pleistocene. If the environmental tolerances of taxa remained the same from the Late Pleistocene, then the Holocene distribution of fossil taxa should be similar to the modern distribution and the Pleistocene distribution should be different, depending on the tolerances of the taxa.

Both *Blarina* and *Sorex* have modern distributions that reflect humid environments. In Texas, *Blarina* is restricted to east Texas, with a relict population in Bastrop. *Sorex* is not found in Texas today, though several species are found near the borders. In the Pleistocene, the range of *Blarina* was farther west than today (Figure 4.14), and there were numerous sites that are reported to include fossils of *Sorex* (Figure 4.15). As recently as the Holocene, *Blarina* occupied a range much farther west than it does today. The FAUNMAP II database has records of *Sorex* in Texas as late as the Holocene (Graham and Lundelius, 2010). The sites indicated as Holocene in Figure 4.15 are based on the youngest age dates in the database. It is uncertain from the database alone whether the *Sorex* was found in association with the youngest dated material, nor is there certainty in the dating for all sites. These would be ideal sites to re-date, or directly date the *Sorex* material to determine when *Sorex* was extirpated from Texas.

Notiosorex is the only shrew for which the distribution of Quaternary sites lies within the modern distribution (Figure 4.12). Currently, the ranges of *Notiosorex* and

Blarina only overlap in a small area of extreme northeast Texas. They are not found in any Quaternary sites in that area, but were found together at nine different sites in other parts of Texas. *Notiosorex* is generally considered a desert-adapted species and *Blarina* is found in environments that are more humid.

The modern range in Texas of *Notiosorex* overlaps to a greater degree with *Cryptotis* than it does with *Blarina* (Figure 4.23). The co-occurrence of *Notiosorex* and *Cryptotis* goes back to the Irvingtonian at Fyllan Cave (Taylor, 1982 and Winkler and Gose, 2003). *Cryptotis* is absent from most of the Edwards Plateau today. However, during the Holocene *Cryptotis* was found at four sites outside of its modern range. At Hall's Cave, which has the best stratigraphy of the sites on the Edwards Plateau, *Cryptotis* was present until about 500 radiocarbon years before present (rcybp) (Toomey, 1993). *Cryptotis* also was found in association with historically dated sediments at Longhorn Cave, Lower Sloth Cave, and Rattlesnake Cave (Graham and Lundelius, 2010). Lower Sloth Cave is on the border of New Mexico, far to the west of the "modern" distribution. If the identifications and dating of *Cryptotis* at those sites are correct then the present-day range of *Cryptotis* was established relatively recently. This also adds evidence that the environmental preferences of extant shrews are ephemeral.

Several potential hypotheses can be proposed to account for the differences in the ranges of shrews from the Quaternary to the present. First, the environmental conditions could have been more favorable, promoting a greater diversity of shrews in a given geographic region. That argument was hypothesized as an explanation for why certain species that are found hundreds or thousands of kilometers apart today are found together in the Pleistocene (FAUNMAP Working Group, 1996). Second, the

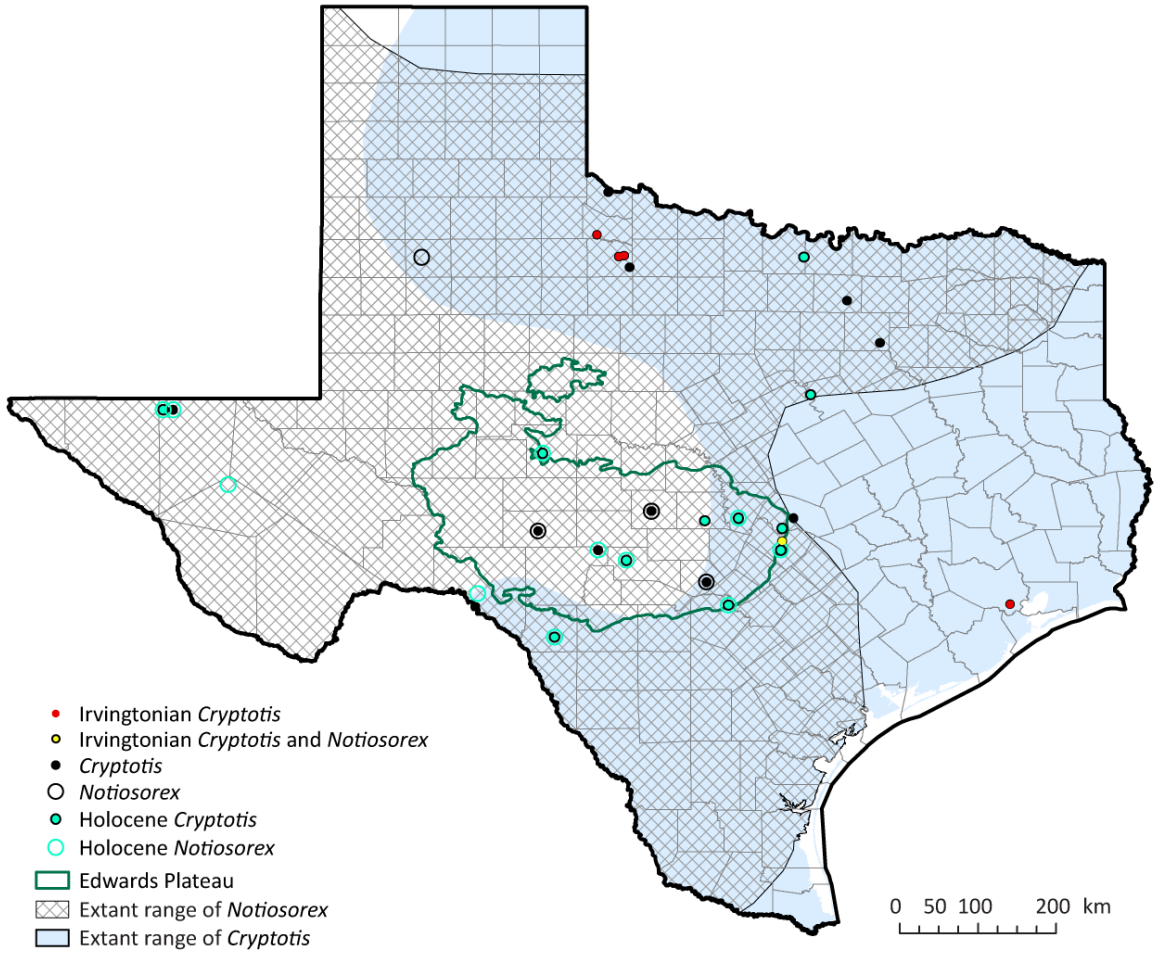


Figure 4.23. Distribution of Quaternary sites with *Cryptotis* and *Notiosorex* in Texas shown with the modern ranges of the genera. Note the single Irvingtonian site, Fyllan Cave, that had both genera.

environmental tolerances of the shrews could have evolved since the Pleistocene, and they are now tolerant of a different or narrower range of environments or conditions than they were in the Quaternary. Neither of these hypotheses is mutually exclusive. Environmental conditions could have changed and the shrews could be evolving away from a range of tolerances that are not fully realized today. The first step towards falsifying one of these hypotheses is to use independent data that suggest what the environmental conditions were like when the fossils were deposited.

Multiple independent paleoclimate data sources exist for the Edwards Plateau. This makes the Edwards Plateau the most appropriate region in Texas for testing these hypotheses. One key site is Felton Cave. That cave has a narrow age range of 7500-7800 rcybp. *Blarina*, *Cryptotis*, and *Notiosorex* were identified from the deposit (Lundelius, 1967). This cave is located on the western part of the Edwards Plateau. The paleoenvironmental data from pollen, C13 isotopes, magnetic susceptibility, speleothems, and sedimentation all indicate that this was a period of dry conditions on the Edwards Plateau (Toomey et al., 1993; Nordt et al., 1994; Elwood and Gose, 2006; Musgrove et al., 2001; Cooke, 2005; Boulter et al., 2010). Conditions were at least as arid as today, and around 7500 years ago, a transition to the driest conditions of the Holocene began. *Blarina*, *Cryptotis*, and *Notiosorex* also were present at Hall's Cave from approximately contemporaneous strata (Toomey, 1993; Chapter 2). If conditions on the Edwards Plateau were similar to today, or more arid, and these shrews were contemporaneous, then environmental conditions found on the plateau today may not be limiting the current range of these taxa. If environmental conditions are not the sole factor influencing the range of those shrews, then it must be possible that other ecological factors besides the environmental conditions are shaping the current distribution of shrews in Texas. Therefore, it will be challenging to predict the effect of changing

environmental conditions on the distribution of those shrew taxa, and potentially other mammals as well.

This is the first part of a long-term study to attempt to understand the relationship between climate and the environmental tolerances of mammals. As databases are expanded and additional types of data are integrated into them, better analyses of the paleobiogeography of mammals will be possible. I urge caution in assigning paleoenvironmental interpretations based solely on the mammal fauna. The Edwards Plateau provides an important example of the need to have multiple independent paleoclimate proxies to make appropriate interpretations about past environments and the distribution of mammals.

Another important aspect of working with databases like FAUNMAP is an appreciation of the potential problems with the identifications of taxa. Several studies that examined the changes in species ranges from the Pleistocene to the Holocene (FAUNMAP Working Group, 1996, Lyons, 2005) will have biased results if species were identified using geographic assumptions. There is some utility in using generic identifications. First, identification to genus does not conceal assumptions about how the fossils were identified as long as the generic identifications are based upon morphological characters. Second, there are positive results that can be gained from working with generic-level identifications. The ranges of the genera of shrews show significant differences between the present and other times during the Pleistocene and Holocene. A study of the range shifts in mammals across North America found significant differences between Pleistocene and the present distributions even when working at the generic level (Cannon, 2004). It is important to consider whether species identifications are required for the type of question being asked (Bell et al., 2010). If fossils cannot be identified to species without geographic assumptions, then they should be left as generic

identifications, or the most refined taxonomic level for which morphological characters can provide the identification.

Appendix A: List of extant specimens examined for character analysis.

Name	ID number[1]	Name	ID number
Blarina brevicauda	TCWC 20636	*Cryptotis magna*	TCWC 41950
Blarina brevicauda	TCWC 23684	*Cryptotis magna*	TCWC 41951
Blarina brevicauda	TCWC 29730	*Cryptotis magna*	TCWC 41952
Blarina brevicauda	TCWC 29730	*Cryptotis mexicana*	TCWC 44502
Blarina brevicauda	TCWC 50105	*Cryptotis mexicana*	TCWC 45106
Blarina brevicauda	TMM M-315	*Cryptotis parva*	TCWC 30491
Blarina brevicauda	TMM M-6585	*Cryptotis parva*	TCWC 34980
Blarina carolinensis	TCWC 16192	*Cryptotis parva*	TCWC 45855
Blarina carolinensis	TCWC 27622	*Cryptotis parva*	TCWC 50179
Blarina carolinensis	TCWC 27626	*Cryptotis parva*	TCWC 50181
Blarina carolinensis	TCWC 33339	*Cryptotis parva*	TCWC 50182
Blarina carolinensis	TCWC 33344	*Megasorex gigas*	TCWC 41958
Blarina carolinensis	TCWC 33359	*Megasorex gigas*	TCWC 5826
Blarina carolinensis	TCWC 33361	*Megasorex gigas*	TCWC 5828
Blarina carolinensis	TCWC 6624	*Megasorex gigas*	TCWC 5829
Blarina hylophaga	TCWC 30396	*Megasorex gigas*	TCWC 5830
Blarina hylophaga	TCWC 31837	*Notiosorex crawfordi*	TCWC 2335
Blarina hylophaga	TCWC 50133	*Notiosorex crawfordi*	TK 7521
Blarina hylophaga	TCWC 50173	*Notiosorex crawfordi*	TK 75222
Blarina hylophaga	TCWC 51797	*Notiosorex crawfordi*	TTU 31606
Blarina hylophaga	TCWC 53302	*Notiosorex crawfordi*	TTU 6323
Blarina hylophaga	TCWC 53306	*Notiosorex crawfordi*	TTU 92929
Crocidura hildegardeae	USNM 535332	*Notiosorex crawfordi*	TTU 9728
Crocidura hirta	USNM 260771	*Sorex arcticus*	TCWC 20638
Crocidura hirta	USNM 295189	*Sorex arcticus*	TCWC 50196
Crocidura mutesae	USNM 537662	*Sorex bendirii*	TCWC 25881
Crocidura nanilla	USNM 401327	*Sorex bendirii*	TCWC 26649
Crocidura russula	TMM M-4130	*Sorex cinereus*	TCWC 16235
Crocidura russula	USNM 084736	*Sorex cinereus*	TCWC 20642
Crocidura russula	USNM 152485	*Sorex cinereus*	TCWC 26977
Crocidura russula	USNM 470582	*Sorex fumeus*	TCWC 20652
Crocidura russula	USNM 476080	*Sorex fumeus*	TCWC 6564
Cryptotis goldmani	TCWC 5665	*Sorex trowbridgii*	TCWC 45855
Cryptotis goldmani	TCWC 5573	*Sorex vagrans*	TCWC 20646
Cryptotis goldmani	TCWC 5575	*Sorex vagrans*	TCWC 20650
Cryptotis goldmani	TCWC 41948		

[1]Collection abbreviations: TCWC Texas Cooperative Wildlife Collection; TMM Texas Memorial Museum; TTU/TK Texas Tech; USNM Smithsonian.

Appendix B: List of specimens identified from Hall's Cave.

TMM	Original Identification	New Identification
521	*Sorex cinereus*	*Sorex*
2732	*Sorex* cf. *haydeni*	*Sorex*
3805	*Sorex cinereus* or *haydeni*	*Sorex*
5778	*Sorex*	Soricidae
5785	*Sorex*	?
5847	*Sorex*	*Sorex*
10814	*Cryptotis parva*	*Cryptotis parva*
10815	*Cryptotis parva*	*Cryptotis parva*
10816	*Notiosorex crawfordi*	*Notiosorex*
10817	*Cryptotis parva*	Blarinini
10818	*Blarina carolinensis*	*Blarina*
10827	*Blarina carolinensis*	*Blarina*
10828	*Blarina carolinensis*	*Blarina brevicauda*
10829	*Blarina carolinensis*	*Blarina*
10830	*Blarina carolinensis*	*Blarina hylophaga*
10831	*Blarina carolinensis*	*Blarina*
10832	*Blarina carolinensis*	Node 3
11045	*Blarina carolinensis*	*Blarina*
11046	*Blarina carolinensis*	*Blarina*
11047	*Blarina carolinensis*	*Blarina carolinensis*
11048	*Blarina carolinensis*	?
11049	*Blarina carolinensis*	Blarinini
11050	*Blarina carolinensis*	*Blarina*
11051	*Blarina carolinensis*	?
11052	*Blarina carolinensis*	?
11053	*Sorex*	Soricidae
11084	*Blarina carolinensis*	Blarinini
11085	*Cryptotis parva*	*Cryptotis parva*
11086	*Cryptotis parva*	*Cryptotis parva*
11107	*Blarina carolinensis*	*Blarina*
11108	*Blarina carolinensis*	*Blarina carolinensis*
11332	*Notiosorex crawfordi*	*Notiosorex*
11434	*Notiosorex crawfordi*	Soricidae
11601	*Cryptotis parva*	*Cryptotis*
11602	*Blarina carolinensis*	*Blarina*
11603	*Blarina carolinensis*	*Blarina*
11604	*Cryptotis parva*	Blarinini

TMM	Original ID	New Identification
11651	*Blarina carolinensis*	*Blarina*
11652	*Cryptotis parva*	*Cryptotis parva*
11653	*Notiosorex crawfordi*	*Notiosorex*
11654	*Notiosorex crawfordi*	Notiosoricini
11659	*Notiosorex crawfordi*	*Notiosorex*
11660	*Notiosorex crawfordi*	*Notiosorex*
11661	*Notiosorex crawfordi*	*Notiosorex*
11662	*Notiosorex crawfordi*	*Notiosorex*
11663	*Notiosorex crawfordi*	*Notiosorex*
11664	*Notiosorex crawfordi*	*Notiosorex*
11665	*Notiosorex crawfordi*	*Notiosorex*
11666	*Notiosorex crawfordi*	*Notiosorex*
11667	*Notiosorex crawfordi*	*Notiosorex*
11668	*Notiosorex crawfordi*	Notiosoricini
11669	*Notiosorex crawfordi*	Notiosoricini
11670	*Notiosorex crawfordi*	*Cryptotis parva*
11671	*Notiosorex crawfordi*	*Notiosorex*
11672	*Notiosorex crawfordi*	*Notiosorex*
11673	*Notiosorex crawfordi*	*Notiosorex*
11674	*Notiosorex crawfordi*	Notiosoricini
11675	*Notiosorex crawfordi*	*Notiosorex*
11688	*Blarina carolinensis*	*Blarina*
11689	*Blarina carolinensis*	Blarinini
11705	*Notiosorex crawfordi*	*Notiosorex*
12027	*Blarina carolinensis*	*Blarina*
12045	*Cryptotis parva*	*Cryptotis parva*
12046	*Cryptotis parva*	*Cryptotis parva*
12047	*Cryptotis parva*	*Cryptotis parva*
12048	*Cryptotis parva*	*Cryptotis parva*
12049	*Blarina carolinensis*	*Blarina*
12050	*Blarina carolinensis*	*Blarina hylophaga*
12051	*Blarina carolinensis*	*Blarina*
12052	*Blarina carolinensis*	Blarinini
12053	*Blarina carolinensis*	*Blarina*
12054	*Blarina carolinensis*	Blarinini
12055	*Blarina carolinensis*	Blarinini

Appendix C: Quaternary sites in Texas from the FAUNMAP II database

Name	Type	Age - Young	Age - Old
'The' Cave	cave	Post-Rancholabrean	Post-Rancholabrean
10th and Congress Gator	non-cave	Post-Rancholabrean	Post-Rancholabrean
41Bx180	non-cave	Post-Rancholabrean	Post-Rancholabrean
41Bx228	non-cave	Post-Rancholabrean	Post-Rancholabrean
41NU102	non-cave	Post-Rancholabrean	Post-Rancholabrean
41NU103	non-cave	Post-Rancholabrean	Post-Rancholabrean
41TG91	non-cave	Post-Rancholabrean	Post-Rancholabrean
41WY50	non-cave	Post-Rancholabrean	Rancholabrean
41WY62	non-cave	Rancholabrean	Rancholabrean
41WY65	non-cave	Rancholabrean	Rancholabrean
Antelope Creek 22	non-cave	Post-Rancholabrean	Post-Rancholabrean
Antelope Creek 22A	non-cave	Post-Rancholabrean	Post-Rancholabrean
Antelope Creek 24	non-cave	Post-Rancholabrean	Post-Rancholabrean
Aransas Pass 1	non-cave	Rancholabrean	Rancholabrean
Aransas Pass 2	non-cave	Rancholabrean	Rancholabrean
Aransas River	non-cave	Rancholabrean	Rancholabrean
Aransas River	non-cave	Rancholabrean	Rancholabrean
Arenosa Shelter	cave	Post-Rancholabrean	Rancholabrean
Aubrey [41DN479]	non-cave	Rancholabrean	Rancholabrean
Avenue Site	non-cave	Rancholabrean	Rancholabrean
Ayala [79D5-1]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Aycock Farm	non-cave	Rancholabrean	Rancholabrean
Baker Cave [41VV213]	cave	Post-Rancholabrean	Post-Rancholabrean
Barron's Creek	non-cave	Rancholabrean	Rancholabrean
Barton Springs Road	cave	Post-Rancholabrean	Post-Rancholabrean
Bastrop County Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Batt Gravel Pit	non-cave	Pleistocene	Rancholabrean
Bear Creek Shelter [41HI17]	cave	Post-Rancholabrean	Post-Rancholabrean
Bell [41HL65]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Ben Franklin	non-cave	Post-Rancholabrean	Rancholabrean
Benjamin	non-cave	Rancholabrean	Rancholabrean
Berclair	non-cave	Rancholabrean	Rancholabrean
Berclair Terrace Site 1 [TMM-31019]	non-cave	Rancholabrean	Rancholabrean
Bergstrom AFB	non-cave	Rancholabrean	Rancholabrean
Bering Sinkhole	cave	Post-Rancholabrean	Post-Rancholabrean
Big Motha Cave	cave	Rancholabrean	Rancholabrean
Big Rock Shelter [41HE1]	cave	Post-Rancholabrean	Post-Rancholabrean
Big Shell Banks	non-cave	Rancholabrean	Rancholabrean
Big Spring	non-cave	Rancholabrean	Rancholabrean
Bishop Gravel Pit No.1	non-cave	Rancholabrean	Rancholabrean

Name	Type	Age - Young	Age - Old
Bishop Gravel Pit No.2	non-cave	Rancholabrean	Rancholabrean
Bishop Gravel Pit No.3	non-cave	Rancholabrean	Rancholabrean
Bishop Pit No. 2	non-cave	Rancholabrean	Rancholabrean
Bivins Ranch	non-cave	Rancholabrean	Rancholabrean
Blanco Creek	non-cave	Rancholabrean	Rancholabrean
Blanco Creek	non-cave	Rancholabrean	Rancholabrean
Blanconia Bridge	non-cave	Rancholabrean	Rancholabrean
Blum Shelter	cave	Post-Rancholabrean	Post-Rancholabrean
Boggy Creek	non-cave	Rancholabrean	Rancholabrean
Bone Springs Draw	non-cave	Rancholabrean	Rancholabrean
Bonfire Cave	cave	Post-Rancholabrean	Rancholabrean
Borrego Creek	non-cave	Rancholabrean	Rancholabrean
Borrego Creek	non-cave	Rancholabrean	Rancholabrean
Britton Site	non-cave	Post-Rancholabrean	Post-Rancholabrean
Brooks Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Brynjulfson Cave	non-cave	Rancholabrean	Rancholabrean
Buckner Ranch 3	non-cave	Rancholabrean	Rancholabrean
Burial Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Burnett Ranch	non-cave	Irvingtonian	Irvingtonian
Burris [41VT66]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Buzzard Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Buzzard's Roost	non-cave	Post-Rancholabrean	Post-Rancholabrean
C.E. Evans Farm	non-cave	Rancholabrean	Rancholabrean
Caldwell Ranch	cave	Rancholabrean	Rancholabrean
Callo del Oso	non-cave	Rancholabrean	Rancholabrean
Cameron	non-cave	Rancholabrean	Rancholabrean
Canadian River	non-cave	Rancholabrean	Rancholabrean
Canyon	non-cave	Rancholabrean	Rancholabrean
Carpenter Farm	non-cave	Rancholabrean	Rancholabrean
Carrol Creek	non-cave	Rancholabrean	Rancholabrean
Carter Draw	non-cave	Rancholabrean	Rancholabrean
Cartwright Ranch	non-cave	Rancholabrean	Rancholabrean
Casa Blanca Ranch	non-cave	Rancholabrean	Rancholabrean
Cascade Caverns	cave	Post-Rancholabrean	Post-Rancholabrean
Cave Without A Name	cave	Rancholabrean	Rancholabrean
Caverns of Sonora	cave	Post-Rancholabrean	Post-Rancholabrean
Cayuga	non-cave	Rancholabrean	Rancholabrean
Centipede Cave	cave	Rancholabrean	Rancholabrean
Ceremonial Cave	cave	Post-Rancholabrean	Rancholabrean
Cinnabar Mine	cave	Rancholabrean	Rancholabrean
City Dump	non-cave	Rancholabrean	Rancholabrean
City Hall Muskox	non-cave	Rancholabrean	Rancholabrean
Clamp Cave	cave	Rancholabrean	Rancholabrean
Cleaver [41BO15]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Coahoma	non-cave	Rancholabrean	Rancholabrean

Name	Type	Age - Young	Age - Old
Collier [41HL64]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Collins Site	non-cave	Rancholabrean	Rancholabrean
Colorado Street Site	non-cave	Rancholabrean	Rancholabrean
Conejo Shelter	cave	Rancholabrean	Rancholabrean
Conner [41HC7]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Coontail Spin	cave	Rancholabrean	Rancholabrean
Copperhead [41BO13]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Cove Harbor	non-cave	Rancholabrean	Rancholabrean
Cowan Ranch	non-cave	Rancholabrean	Rancholabrean
Coyote Lake	non-cave	Rancholabrean	Rancholabrean
Crews Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Crumley Site	non-cave	Post-Rancholabrean	Post-Rancholabrean
Cueva Quebrada	cave	Rancholabrean	Rancholabrean
Dalton Lane	non-cave	Rancholabrean	Rancholabrean
Damp Cave	cave	Rancholabrean	Rancholabrean
Dan Fox Ranch	non-cave	Rancholabrean	Rancholabrean
Dead Man's Hole	non-cave	Post-Rancholabrean	Post-Rancholabrean
Deadman's Shelter [41SW23]	cave	Post-Rancholabrean	Post-Rancholabrean
Deep	non-cave	Post-Rancholabrean	Rancholabrean
Del Valle	non-cave	Rancholabrean	Rancholabrean
Devil's Hollow [41TV38]	non-cave	Post-Rancholabrean	Rancholabrean
Devil's Mouth	non-cave	Post-Rancholabrean	Post-Rancholabrean
Dieceocho Creek	non-cave	Irvingtonian	Irvingtonian
Double Mountain Fork Brazos River	non-cave	Rancholabrean	Rancholabrean
Dreyer Farm	non-cave	Rancholabrean	Rancholabrean
Dry Creek	non-cave	Irvingtonian	Irvingtonian
Dust Cave [C-09]	cave	Rancholabrean	Rancholabrean
Dye Creek	non-cave	Post-Rancholabrean	Post-Rancholabrean
E & A Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Eagle Cave	cave	Rancholabrean	Rancholabrean
Ebaugh Gravel Pit	non-cave	Rancholabrean	Rancholabrean
El Sauz Ranch	non-cave	Post-Rancholabrean	Post-Rancholabrean
Fallen Stalagmite Cave	cave	Rancholabrean	Rancholabrean
Farrish Ranch	non-cave	Rancholabrean	Rancholabrean
Fawcett's Cave	cave	Post-Rancholabrean	Rancholabrean
Felton Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Fentress	non-cave	Rancholabrean	Rancholabrean
Fern Cave	cave	Post-Rancholabrean	Rancholabrean
Finch [A-128]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Fingerprint Cave	cave	Post-Rancholabrean	Rancholabrean
Finis Frost [41SS20]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Footbridge [41CM2]	cave	Post-Rancholabrean	Rancholabrean
Fort Sam Houston	non-cave	Rancholabrean	Rancholabrean
Foster Ranch Cave	cave	Rancholabrean	Rancholabrean

Name	Type	Age - Young	Age - Old
Fowlkes Cave	cave	Post-Rancholabrean	Rancholabrean
Fox's Bend	non-cave	Rancholabrean	Rancholabrean
Fred Dubose Farm	non-cave	Rancholabrean	Rancholabrean
Friesenhahn Cave	cave	Post-Rancholabrean	Rancholabrean
Gilbert [41RA13]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Gosset Bottom Site	non-cave	Post-Rancholabrean	Post-Rancholabrean
Greenhaw [41HY29]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Guitar Estate ?	non-cave	Rancholabrean	Rancholabrean
Gus Peshka Fishing Camp	non-cave	Rancholabrean	Rancholabrean
Hall's Cave	cave	Post-Rancholabrean	Rancholabrean
Harrell Site	non-cave	Post-Rancholabrean	Post-Rancholabrean
Harris Ranch	non-cave	Rancholabrean	Rancholabrean
Harvey Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Heard Ranch	non-cave	Rancholabrean	Rancholabrean
Heard Ranch	non-cave	Rancholabrean	Rancholabrean
Hickmunton Corner	non-cave	Post-Rancholabrean	Post-Rancholabrean
High Island	non-cave	Rancholabrean	Rancholabrean
Hinds Cave [41VV456]	cave	Post-Rancholabrean	Rancholabrean
Hitzfelder's Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Holdsworth [41ZV14]	cave	Post-Rancholabrean	Post-Rancholabrean
Holloway Ranch	non-cave	Rancholabrean	Rancholabrean
Hoover [P-96]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Horn Shelter #2	cave	Rancholabrean	Rancholabrean
Howard Ranch	non-cave	Rancholabrean	Rancholabrean
Hueco Mountains Cave 10	cave	Post-Rancholabrean	Post-Rancholabrean
Hueco Mountains Cave 9	cave	Post-Rancholabrean	Post-Rancholabrean
Hueco Tanks No. 1	non-cave	Post-Rancholabrean	Rancholabrean
Hueco Tanks State Hist. Pk. [41EP2]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Humble Bison Site	non-cave	Rancholabrean	Rancholabrean
Humble Mammoth Site	non-cave	Rancholabrean	Rancholabrean
Ingleside	non-cave	Rancholabrean	Rancholabrean
Jackson Farm	non-cave	Rancholabrean	Rancholabrean
Jackson Ranch	non-cave	Rancholabrean	Rancholabrean
Javelina Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Jetta Court [41TV151]	non-cave	Post-Rancholabrean	Rancholabrean
Jumbo Lake	non-cave	Rancholabrean	Rancholabrean
Kent Crane Site No. 2	non-cave	Pleistocene	Rancholabrean
Kincaid Shelter	cave	Post-Rancholabrean	Rancholabrean
Kitchen Door	cave	Irvingtonian	Irvingtonian
Kocurek Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Kyle [41HI1]	cave	Post-Rancholabrean	Post-Rancholabrean
L.L. Winterbauer Site	non-cave	Post-Rancholabrean	Post-Rancholabrean
Lagarto Creek 1	non-cave	Rancholabrean	Rancholabrean
Lagarto Creek 2	non-cave	Rancholabrean	Rancholabrean

Name	Type	Age - Young	Age - Old
Lake Creek [A48]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Lake Theo	non-cave	Rancholabrean	Rancholabrean
Lampkin Farm	non-cave	Rancholabrean	Rancholabrean
LaPaloma Ranch	non-cave	Post-Rancholabrean	Rancholabrean
Lapara Creek	non-cave	Rancholabrean	Rancholabrean
Laubach 1	non-cave	Rancholabrean	Rancholabrean
League Ranch	non-cave	Rancholabrean	Rancholabrean
League Ranch	non-cave	Rancholabrean	Rancholabrean
Leo Boatwright Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Leon River	non-cave	Rancholabrean	Rancholabrean
Levi Shelter	cave	Post-Rancholabrean	Rancholabrean
Lewisville Site	non-cave	Rancholabrean	Rancholabrean
Lipscomb Bison Quarry	non-cave	Rancholabrean	Rancholabrean
Little 38 Oaks Mine	non-cave	Rancholabrean	Rancholabrean
Little Brazos River	non-cave	Rancholabrean	Rancholabrean
Little River	non-cave	Rancholabrean	Rancholabrean
Little River	non-cave	Rancholabrean	Rancholabrean
Locality 31538	non-cave	Rancholabrean	Rancholabrean
Loeve-Fox Site	non-cave	Rancholabrean	Rancholabrean
Longhorn Cave	cave	Post-Rancholabrean	Rancholabrean
Los Coyotes	non-cave	Rancholabrean	Rancholabrean
Lower Sloth Cave	cave	Post-Rancholabrean	Rancholabrean
Lubbock Lake	non-cave	Post-Rancholabrean	Rancholabrean
Lucas Ranch	non-cave	Rancholabrean	Rancholabrean
Lucas Ranch	non-cave	Rancholabrean	Rancholabrean
Lucas Ranch	non-cave	Rancholabrean	Rancholabrean
Macs Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Magnolia Booster Station	non-cave	Post-Rancholabrean	Post-Rancholabrean
Manton Miller [41DT]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Mayfield Ranch	non-cave	Irvingtonian	Irvingtonian
McKinzie [41NU221]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Medford Ranch [41HC10]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Medio Creek	non-cave	Rancholabrean	Rancholabrean
Miami	non-cave	Post-Rancholabrean	Rancholabrean
Mile Canyon Shelter	cave	Post-Rancholabrean	Post-Rancholabrean
Miller's Cave	cave	Post-Rancholabrean	Rancholabrean
Minerva Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Minnow Sparks [41FK12]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Mirando City Oilfield	non-cave	Rancholabrean	Rancholabrean
Monk's Cave [41RK84]	cave	Post-Rancholabrean	Post-Rancholabrean
Montell Shelter	cave	Post-Rancholabrean	Post-Rancholabrean
Monument Lake	non-cave	Rancholabrean	Rancholabrean
Moore Pit	non-cave	Rancholabrean	Rancholabrean
Morhiss Mound	non-cave	Rancholabrean	Rancholabrean
Mosquito Cave	cave	Rancholabrean	Rancholabrean

Name	Type	Age - Young	Age - Old
Murrah Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Natural Bridge Cave	cave	Rancholabrean	Rancholabrean
Navar Ranch No. 13	non-cave	Post-Rancholabrean	Rancholabrean
New Braunfels	non-cave	Rancholabrean	Rancholabrean
Nobles Point	non-cave	Rancholabrean	Rancholabrean
Nollin Ranch	non-cave	Rancholabrean	Rancholabrean
Nollin Ranch	non-cave	Rancholabrean	Rancholabrean
North Sulphur River	non-cave	Post-Rancholabrean	Rancholabrean
North Tule Creek	non-cave	Rancholabrean	Rancholabrean
Nueces River	non-cave	Rancholabrean	Rancholabrean
O'Brian Ranch	non-cave	Rancholabrean	Rancholabrean
O'Brian Ranch	non-cave	Rancholabrean	Rancholabrean
O'Brian Ranch	non-cave	Rancholabrean	Rancholabrean
Oak Springs Elementary School	non-cave	Rancholabrean	Rancholabrean
Oblate Site	cave	Post-Rancholabrean	Post-Rancholabrean
Old Glory	non-cave	Rancholabrean	Rancholabrean
Old River Road Locality #1	non-cave	Post-Rancholabrean	Post-Rancholabrean
Onion Creek Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Parida Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Pearland	non-cave	Rancholabrean	Rancholabrean
Pease Park	non-cave	Post-Rancholabrean	Post-Rancholabrean
Perry-Calk Site	non-cave	Rancholabrean	Rancholabrean
Pickett Ruin [A-116]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Pickup Pueblo	non-cave	Post-Rancholabrean	Post-Rancholabrean
Pictograph Shelter	cave	Post-Rancholabrean	Post-Rancholabrean
Pilot Knob	non-cave	Rancholabrean	Rancholabrean
Pitts Bridge Bootherium Locality [3]	non-cave	Rancholabrean	Rancholabrean
Pittsbridge	non-cave	Rancholabrean	Rancholabrean
Pittsbridge	non-cave	Rancholabrean	Rancholabrean
Plainview	non-cave	Post-Rancholabrean	Post-Rancholabrean
Plainview East	non-cave	Rancholabrean	Rancholabrean
Plainview North	non-cave	Rancholabrean	Rancholabrean
Plainview Quarry	non-cave	Rancholabrean	Rancholabrean
Port Isabel	non-cave	Rancholabrean	Rancholabrean
Port Sullivan	non-cave	Rancholabrean	Rancholabrean
Pratt Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Quitaque Creek	non-cave	Rancholabrean	Rancholabrean
R.O.	non-cave	Post-Rancholabrean	Post-Rancholabrean
Rattlesnake Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Reagen Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Rector Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Red Bluff	non-cave	Rancholabrean	Rancholabrean
Red Bluff Dam	non-cave	Rancholabrean	Rancholabrean

Name	Type	Age - Young	Age - Old
Red Mud Creek	non-cave	Rancholabrean	Rancholabrean
Redfish Bay	non-cave	Rancholabrean	Rancholabrean
Rex Rodgers [41BI42]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Rhodes Point	non-cave	Rancholabrean	Rancholabrean
Rich Lake	non-cave	Rancholabrean	Rancholabrean
Ridge Top	non-cave	Rancholabrean	Rancholabrean
Rio Grande	non-cave	Rancholabrean	Rancholabrean
Rock Creek	non-cave	Irvingtonian	Irvingtonian
Rock Creek Equus Beds	non-cave	Irvingtonian	Irvingtonian
Rockport	non-cave	Rancholabrean	Rancholabrean
Rocky Creek	non-cave	Post-Rancholabrean	Post-Rancholabrean
Runnels-Pierce Ranch	non-cave	Rancholabrean	Rancholabrean
Rush Creek	non-cave	Rancholabrean	Rancholabrean
Sabine River Site #1	non-cave	Post-Rancholabrean	Post-Rancholabrean
Saint David's Hospital	non-cave	Rancholabrean	Rancholabrean
Salt Fork Brazos River	non-cave	Rancholabrean	Rancholabrean
Salt Fork of the Brazos River	non-cave	Rancholabrean	Rancholabrean
Samuelson Farm	non-cave	Post-Rancholabrean	Post-Rancholabrean
San Antonio River	non-cave	Rancholabrean	Rancholabrean
San Antonio River	non-cave	Rancholabrean	Rancholabrean
San Domingo Ranch	non-cave	Rancholabrean	Rancholabrean
San Felipe State Park	non-cave	Rancholabrean	Rancholabrean
San Marcos Riverbank	non-cave	Post-Rancholabrean	Post-Rancholabrean
Sand Springs	non-cave	Rancholabrean	Rancholabrean
Sanford Reservoir	non-cave	Post-Rancholabrean	Post-Rancholabrean
Sanford Reservoir	non-cave	Post-Rancholabrean	Post-Rancholabrean
Sanford Ruin [41HC3]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Schulze Cave	cave	Post-Rancholabrean	Rancholabrean
Scorpion Cave [41ME7]	cave	Post-Rancholabrean	Rancholabrean
Scott Ranch	non-cave	Rancholabrean	Rancholabrean
Seale Pit	non-cave	Rancholabrean	Rancholabrean
Seminole Canyon Cave	cave	Rancholabrean	Rancholabrean
Seminole Sink [41VV620]	cave	Post-Rancholabrean	Rancholabrean
Seymour	non-cave	Rancholabrean	Rancholabrean
Shafter Lake	non-cave	Post-Rancholabrean	Post-Rancholabrean
Shanklin [41WH8]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Sheep Shelter	cave	Post-Rancholabrean	Post-Rancholabrean
Sitter Ranch	non-cave	Post-Rancholabrean	Post-Rancholabrean
Skeen Farm	non-cave	Rancholabrean	Rancholabrean
Slaton Quarry	non-cave	Irvingtonian	Irvingtonian
Smart Ranch Capromeryx Locality	non-cave	Rancholabrean	Rancholabrean
Smith Rockshelter	cave	Post-Rancholabrean	Post-Rancholabrean
South Padre Island	non-cave	Rancholabrean	Rancholabrean
South Sulphur River	non-cave	Rancholabrean	Rancholabrean

Name	Type	Age - Young	Age - Old
Spider Mountain Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Stansbury Site	non-cave	Post-Rancholabrean	Post-Rancholabrean
Starveout Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Stout Mammoth	non-cave	Rancholabrean	Rancholabrean
Strong [41CG31]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Sulfur Creek	non-cave	Rancholabrean	Rancholabrean
Sulfur Creek	non-cave	Rancholabrean	Rancholabrean
Sullivan's Bridge	non-cave	Rancholabrean	Rancholabrean
Susquehanna West Gypsum Quarry	non-cave	Rancholabrean	Rancholabrean
Swan Lake [41AS16]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Swenson	non-cave	Rancholabrean	Rancholabrean
T.M. Sanders Site	non-cave	Post-Rancholabrean	Post-Rancholabrean
Tank Trap Wash No. 1	non-cave	Rancholabrean	Irvingtonian
Testudo Tube Cave	cave	Rancholabrean	Rancholabrean
Tommelson Creek	non-cave	Rancholabrean	Rancholabrean
Toyah Mammoth	non-cave	Rancholabrean	Rancholabrean
Trinity River	non-cave	Rancholabrean	Rancholabrean
Trinity Street	non-cave	Rancholabrean	Rancholabrean
Trout Creek	non-cave	Rancholabrean	Rancholabrean
Twilla [41HL1]	non-cave	Post-Rancholabrean	Post-Rancholabrean
Upper Sloth Cave [TTu-Tex-2]	cave	Post-Rancholabrean	Rancholabrean
Valley Farms	non-cave	Rancholabrean	Rancholabrean
Vinyard Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Vitek Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Waco	non-cave	Rancholabrean	Rancholabrean
Wallace Farm	non-cave	Rancholabrean	Rancholabrean
Waller Creek Terrace	non-cave	Rancholabrean	Rancholabrean
Welder Wildlife Refuge	non-cave	Post-Rancholabrean	Post-Rancholabrean
Wharton Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Whelan Site	non-cave	Post-Rancholabrean	Post-Rancholabrean
Wilkenson Ranch	non-cave	Rancholabrean	Rancholabrean
Willamar	non-cave	Rancholabrean	Rancholabrean
William's Cave	cave	Post-Rancholabrean	Post-Rancholabrean
Wilson-Leonard Site	non-cave	Post-Rancholabrean	Rancholabrean
Winchester	non-cave	Rancholabrean	Rancholabrean
Winnie's Mound [41BU17]	non-cave	Post-Rancholabrean	Rancholabrean
Wright Brothers Gravel Pit	non-cave	Rancholabrean	Rancholabrean
Wunderlich [41CM3]	non-cave	Post-Rancholabrean	Rancholabrean
Wunderlich Site	cave	Post-Rancholabrean	Post-Rancholabrean
Yarbrough Site	non-cave	Post-Rancholabrean	Post-Rancholabrean
Yellowhouse Canyon	non-cave	Rancholabrean	Rancholabrean
Zesch Cave	cave	Rancholabrean	Rancholabrean
Zopilote [41VV216]	cave	Post-Rancholabrean	Post-Rancholabrean

Appendix D: Collections queried for shrews from the MaNIS database.

American Museum of Natural History (AMNH) - Mammals
Arctos - Division of Mammals, Museum of Southwestern Biology, Albuquerque, NM.
Arctos - MVZ Mammal Catalog
Arctos - MVZ Milton Hildebrand Collection
Arctos - Mammal tissues, Division of Genomic Resources, UNM, Albuquerque, NM.
Arctos - University of Alaska Museum, Mammal Collection
Arctos - Western New Mexico University Mammal Collection
California Academy of Sciences (CAS) - Mammal Collection Catalog
Cornell University Museum of Vertebrates (CUMV) - Mammal Collection
Field Museum - FMNH Mammals Collections
Florida Museum of Natural History (UF) - Mammal specimens
Humboldt State University - Humboldt State University, Department of Wildlife
Illinois State University - Illinois State University Mammals Collection
James R. Slater Museum (PSM) - Terrestrial vertebrates
Los Angeles County Museum of Natural History (LACM) - Vertebrate specimens
Louisiana State University Museum of Natural Science - Mammal specimens
MCZ-Harvard University Provider - MCZ Mammalogy Collection
Michigan State University Museum (MSUM) - Vertebrate specimens
Museum of Texas Tech University (TTU) - Mammal specimens
National Museum of Natural History, Smithsonian Institution - NMNH Vertebrate Zoology Mammals Collections
New Mexico Museum of Natural History and Science (NMMNH) - Mammal specimens
New York State Museum - New York State Museum Mammals Collection
Royal Ontario Museum - Mammal specimens
Sam Noble Oklahoma Museum of Natural History - Mammals Specimens
Sam Noble Oklahoma Museum of Natural History - Tissues Specimens
Santa Barbara Museum of Natural History
Texas Cooperative Wildlife Collection (TCWC) - TCWC Vertebrate Collections
UCLA Dickey Collection (UCLA-Dickey) - Bird and Mammal specimens
University Museum of Zoology Cambridge (UMZC) - Zoological specimens
University of Alberta - University of Alberta Museums, Mammalogy Collection
University of Colorado Museum of Natural History - CUMNH Mammal Collection
University of Kansas Biodiversity Institute - Mammal Collection
University of Michigan Museum of Zoology (UMMZ) - Mammal specimens
University of Texas at El Paso - Mammals Specimens
University of Washington Burke Museum - Mammal Specimens
Utah Museum of Natural History (UMNH) - Mammal specimens
Yale University Peabody Museum - Peabody Mammalogy

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Vita

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